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AUDITORY REGIONS OF STREPSIRHINE PRIMATES, TREE SHREWS, ELEPHANT SHREWS, AND LIPOTYPHLOUS INSECTIVORES: AN ONTOGENETIC PERSPECTIVE ON CHARACTER ANALYSIS

by

© Ross Douglas Earle MacPhee

A THESIS

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DEPARTMENT OF ANTHROPOLOGY

EDMONTON, ALBERTA

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THE UNIVERSITY OF ALBERTA

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Auditory Regions of Strepsirhine Primates, Tree Shrews, Elephant Shrews, and Lipotyphlous Insectivores: An Ontogenetic Perspective on Character Analysis submitted by Ross Douglas Earle MacPhee in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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Date August 19/1977

ABSTRACT

The auditory region is considered to be a rich source of taxonomic characters by paleontologists and neontologists specializing in mammals. However, nearly all descriptions of this region in the relevant literature are based on adult conditions. This dissertation attempts to show that a knowledge of conditions during earlier phases of ontogeny can materially assist in the analysis of characters by providing information on how structures develop.

Attention is primarily focused on the development and microanatomy of the strepsirhine basicranium (in particular, on the bony walls of the middle ear and associated soft structures). In order to place results within a meaningful context, similar data are also provided for tupaioids, macroscelideans, and lipotyphlans--the mammals to which primates have been most often compared.

Analysis of the development of otic characters in lorises and lemurs reveals that many of the features utilized to show a sharp contrast between the two major strepsirhine groups have either been overemphasized or misevaluated. Lorises and lemurs differ considerably in the style of pneumatization of the middle ear, and this factor is responsible for most of the observable differences between them in the adult stage. Other features, such as the relationship of the ectotympanic to the petrosal bulla, do not provide clear-cut distinctions either.

It is doubtful that any close relationship between primates and tupaioids can be demonstrated on the basis of their auditory regions. In particular, the embryological and paleonotlogical data suggest that it is quite unlikely that an entotympanic exists or has existed in any undoubted member of Primates.

Similarly, nothing in the development of the macroscelidean bulla suggests that these pecular mammals are related to tree shrews to any significant degree. Members of both groups possess entotympanics but these elements develop in different ways and it is entirely possible that they are not homologous entities.

While the primates may have evolved from ancestral lipotyphlans, there is little in the auditory regions of contemporary insectivores to support this argument. Certainly, it is highly unlikely that one could argue that a particular lipotyphlan group stands in a closer relationship to primates than do other such groups, at least on the basis of otic characters.

In addition to the presentation of materials relevant to character analysis, certain sections of this dissertation are devoted to purely histological and microanatomical studies of otic features. Some attention is also given to the legitimate uses of ontogenetic interpretations in fossil morphology.

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ABBREVIATIONS

AAn	aditus ad antrum
AC	auricular cartilage
AMP	anteromedial process of bulla
AS	alisphenoid
ASC	anterior semicircular canal
AT	auditory tube
BBS	basioccipital-basisphenoidal synchondrosis
BO	basioccipital
BS	basisphenoid
BV	blood vessels
CAT	cartilage of the auditory tube
CEn	caudal entotympanic
CH	ceratohyal
Co	cochlea
CrP	crista parotica
CT	cavum tympani
CTPP	caudal tympanic process of the petrosal
D_1	diverticulum D_1 of the hypotympanic sinus
D_2	diverticulum D_2 of the hypotympanic sinus
D_3	diverticulum D_3 (saccus posterior of the cavum tympani)
D_4	diverticulum D_4 (of the mastoid cavity)
E	ectotympanic
EAM	external acoustic meatus
En	entotympanic (not specific whether rostral or caudal)
EO	exoccipital
EPSq	entoglenoid process of squamosal
ER	epitympanic recess
EWP	epitympanic wing of petrosal
EWS	epitympanic wing of sphenoid
EWSq	epitympanic wing of squamosal
FIn	fossa incudis
FFC	fossula fenestrae cochleae
FMTC	fibrous membrane of the tympanic cavity
G	gonial
HS	hypotympanic sinus
In	incus
IX	glossopharyngeal n.
LS	linea semicircularis
LSC	lateral semicircular canal
M	malleus
Ma	mandible
MC	Meckel's cartilage
MdC	mastoid cavity
MM	membranous meatus
MWF	medial wall of the fossula (fenestrae cochleae)
PaF	parafloccular fossa
PF	piriform fenestra
Ph	pharynx
PM	presumptive tissues of membranous meatus

ABBREVIATIONS -- continued

PP	petrosal plate
Pr	promontory
PrR	processus recessus
PrRA	processus recessus anterior
PrRP	processus recessus posterior
PSC	posterior semicircular canal
Pt	pterygoid (bone)
RC	Reichert's cartilage
REn	rostral entotympanic
RTPP	rostral tympanic process of the petrosal
S	stapes
SCC	superior semicircular canal
SH	stylohyal
Sq	squamosal
TPA	tympanic process of the alisphenoid
TPB	tympanic process of the basisphenoid
TM	tympanic membrane
TT	tegmen tympani
TyM	tympanic mucoid tissue
V	trigeminal n. (stem or ganglion)
V_3	mandibular n.
VII	facial n.
X	vagus n.
XI	accessory n.
XII	hypoglossal n.

CHAPTER ONE

INTRODUCTION

1.1 PROBLEMS AND PERSPECTIVES

1.2 MATERIALS AND TAXONOMIC IDENTIFICATION OF SPECIMENS

- 1.2.1 Materials
- 1.2.2 Taxonomic Identifications

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1.1 PROBLEMS AND PERSPECTIVES

This dissertation presents the results of an extensive investigation into the microanatomy and development of the bony middle ear and related structures in certain strepsirhine prosimians, tree shrews, elephant shrews, and lipotyphlous insectivores. It provides materials, arguments and interpretations relevant to two inquiries:

(1) What is the sequence of development of the several otic structures which, judging from the literature, have attracted the most comment and interest among paleoprimatologists?

(2) Can the ontogeny of these features in modern forms legitimately supplement, improve, or alter our understanding of their evolutionary transformations in fossil antecedents?

Part I of this study addresses the first inquiry, and it provides the essential data required for the profitable treatment of the special topics covered in Part II. As I imply by my choice of words in (1) above, I have not set out to furnish a complete developmental atlas of the entire auditory region, nor can I deal with all the morphological, ontogenetic and evolutionary puzzles this area presents. Instead, I have concentrated on those features which appear to be among the most critical to our understanding of primate phylogeny and classification. Thus the development of tympanic processes and wings, the branchings of the internal carotid, and the ontogeny of pneumatic spaces receive close attention, while other features such as the auditory ossicles and inner ear are either briefly mentioned or ignored.

Not all features and processes singled out for treatment are described in terms of their developmental dynamics. For some topics, such as the growth of tympanic processes and their role in the positioning of the ectotympanic, ontogenetic analysis is obviously warranted. For others, such as the form of the ossicular muscles and routes of nerves, general microanatomical descriptions seemed sufficient. Matters pertinent to description are fully covered in section 1.3.

The purpose of the descriptive part, other than the function it serves in providing the necessary backdrop for Part II, is to fill a major gap in the comparative morphology of the auditory region. Comparative embryologists usually center on the problems offered by the developing chondrocranium, not the osteocranium. Anatomists, on the other hand, rarely deal with other than fully-formed adults. Accordingly, there is a general lack of useful information on the embryonic, perinatal, and juvenile conditions of otic structures. In this study, the post-embryonic, pre-adult period receives special attention. As a result, it has been possible to clarify the poorly-known phases of otic ontogenesis and to relate young to adult conditions in far more detail than has been done before.

Although this work is chiefly meant to be a contribution to the primatological literature, my intent from the outset was to include as many representatives as possible from other groups, for two reasons. First, primate evolutionary biology has suffered, until comparatively recently, from a certain inward-directedness (MARTIN 1968b). However, when one is interested in determining those structural or behavioral features which are distinctive of one order of mammals, it is necessary to make comparisons with members of other orders (cf. CARTMILL 1972, 1974).

Secondly, because of their scale, potentially significant events in ontogeny can be easily missed if attention is restricted to single forms or to closely-related species. The comparative approach helps ensure that the distinctive and the important are rendered conspicuous. Consequently, in Part I tree shrews, elephant shrews and lipotyphlous insectivores are accorded nearly the same degree of attention given to lemurs and lorises, and the few available data on forms in other orders are included wherever pertinent.

Part II provides analyses of the major findings presented in Part I. These analyses emphasize how an ontogenetic perspective on the explanation of form can materially contribute to evolutionary studies (see GOULD 1968). It is clear from the subject matter of this study that it is aimed at providing a surer groundwork for taxonomic studies, and I attempt to show how my findings affect current attitudes towards the evaluation of otic characters.

The value of the material presented in Part II largely depends on one's answer to this important question: what can the embryogeny of structures in living forms establish about their evolution in ancient predecessors? This is a question of many parts, and its answering is further complicated by the extravagant claims once made for embryological data in the context of phylogeny.

No one, I think, would disagree with SIMPSON's (1953:377) formulation of the basic connexion between ontogeny and phylogeny:

> The history of life as it has existed in nature is a vast succession of ontogenies of organisms, all the ontogenies being connected by the fact that each arises with material continuity from one or from two others. This is the objective pattern of evolution, not objective in being now present and verifiable to our senses, which it unfortunately is not, but in being what we otherwise verify as having been the real and physical embodiment of life through the ages. The continuum of ontogenies is phylogeny, and phylogeny has a material pattern traced by the descent of living matter and its development in individuals.

There are two forms of evidence which "otherwise verify" the continuum: the fossil record and the ontogeny of modern individuals. Yet they do so in radically different ways, and accordingly have very different meanings for evolutionary studies. How do they interrelate?

Fossils are the major materials for the study of evolution, a substantive record of descent with modification. They were, in their time, the products of separate ontogenies, and thus part of the material pattern. However, it is obvious from actual cases that it is almost never possible to reconstruct faithfully the entire continuum of ontogenies, for individual fossils only represent specific sampling points within the continuum. For example, since young stages of most ancient mammals are unknown, the mammalian fossil record--read according to its actual entries--is principally the story of adult forms succeeding one another through time. Ancient ontogeny is therefore largely opaque: it must have existed because its products are known to have existed, but, except in rare instances, we simply do not have the proper evidence for reconstructing it in detail.

However, this limit of resolution in paleontology does not have unusual theoretical importance for evolutionary studies. Although truncated, the parts of the continuum we do have still bear their original genetic and temporal relationships to one another. Evolutionary processions can be, and are, legitimately established without complete records of the ontogenetic continuum (however desirable it might be to have such records). The fossil record, however deficient, is a true copy of the forms attained by successive ontogenies in the past. Evolution itself is the result of the modification of ontogenies through time; the existence of fossils permits us to reconstitute the sequence in which those modifications occurred. The ontogenies of living organisms permits nothing of the sort, for they are not exact sequential records of adaptational changes at all, and nothing is more fundamental to the sensible use of embryological data in evolutionary studies than an appreciation of this distinction.

Ontogeny is the result of series of gene-regulated processes which gradually transform, through growth and differentiation, the fertilized egg into a functioning, sexually-mature adult. These processes are both tightly-orchestrated and interactive, and they constitute a remarkably integrated system which is theoretically capable of infinitely repeating itself in much the same way generation after generation. At the same time, everything we know about organic evolution requires that we view ontogenetic systems as no different from other natural systems. They can operate only because conditions permit, and when conditions change they must also if they are to continue. Long-term continuance is possible only if all parts of the life cycle, not just the adult, are well-adapted to their surroundings. Although the cycle cannot be repeated without the successful union of sexually-mature stages (in metazoans, at least), these come to exist only after passing through prior phases of ontogeny, all of which are open to the effects of selection.

This view of ontogeny leads to an important conclusion. If young stages of descendants are not immune to selection, then there is no reason to believe that they are precise repetitions of the young stages of ancestors. Indeed, most lines of evidence point in a contrary direction. Young stages are adaptations (or rather sets of adaptations) to particular environments. Consequently, the ontogeny of any contemporary animal reflects the adaptational history of its phylum only in a peculiar and limited sense. It necessarily builds on what has gone before because successive generations are linked by inheritance. But as any part of the life cycle is open to modification through time, different parts may stay the same or alter in response to selective pressures to any degree consonant with the necessity of preserving an integrated system. Accordingly, in tracing development from egg to adult one does not thereby pass through a series of stages graded from the most ancient to the most recent, but instead through a series of processes which are functionally linked. Just because a feature appears early in ontogeny does not immediately mean that it is historically, i.e. phylogenetically, older than one which appears later, but rather that its function is required or initiated at one time in development and not at another. The ontogenetic 'record' does not preserve adaptations in the order in which they occurred through time, but is instead a picture of how those adaptations of a lineage which are still retained are presently integrated.

Establishing the correct sequence for changes in form, while absolutely vital in tracing the descent of life, is only one task of evolutionary biology. It is equally relevant to establish how changes might have occurred and to select those explanations for changes which best fit the facts. In my opinion, it is here that an embryological perspective offers some help with evolutionary questions, despite the limitations discussed above. Thus I must thoroughly disagree with DAVIS' (1949:71-72) view that an understanding of the "mechanics underlying morphological change", provided by embryology, have little practical interest for the paleontologist because

> ...it fails to get at the core of adaptive evolution. Embryologists may explain post facto the changes in the mechanics of ontogeny that are reflected in an adult adaptation, but evolution demands an explanation of why a given course has been followed far more than it demands detailed clarification of the course actually followed.

It is my contention, as it is of major theorists like DE BEER and GOULD, that how often provides the best insight into why. The embryogeny of structures in living forms provides analogues for, if not replications of, the embryogeny of similar structures in ancestors. It is of course important to signify the adaptive reasons behind change in a lineage, but how can the relative elegance and parsimony of competing explanations of adaptation be evaluated? Surely one criterion is the degree to which they appear to be biologically likely, i.e., what processes or occasions must be invoked in order for the perceived changes to occur. Processes occurring at the genic level are nearly impossible to specify for extinct forms, but at least some headway is possible at the far grosser level of ontogeny. To this extent, embryology has a distinctive role in evolutionary studies which no other science can play.

1.2 MATERIALS AND TAXONOMIC IDENTIFICATIONS OF SPECIMENS

1.2.1 MATERIALS

The materials used for this study include both serially-sectioned and macerated specimens. In the tables accompanying chapters 2 - 7, technical data for each of the thirty sectioned specimens are listed under the following headings:

1. Accession Number (No.). Specimens are designated throughout this paper by their catalogue numbers; the abbreviations preceding catalogue numbers are:

MPIH - Max-Planck-Institut fuer Hirnforschung (Neurobiologische Abteilung, Primatologie), Frankfurt/M-Niederrad.

AI - Anatomisches Institut, J.-W.-Goethe Universitaet, Frankfurt/M-Niederrad.

2. Crown-Rump Length (CRL) and Head Length (HL). These two measurements are defined as follows:

Crown-rump length - apex of head to vent

Head length - tip of nose to rear of skull along a plane passing through the external auditory meatus

The use of these two measurements is both traditional and practical in comparative embryology (AREY 1974). They provide a rough guide to degree of development when one has several specimens of the same species, and they permit comparisons between specimens described in different sources. However, the values listed in the tables should be regarded as no more than approximate. Embryos and fetuses are usually considerably flexed *in utero*, and CRLs in particular should therefore be based on chord lengths. However, nearly all of the specimens described here were processed years before the present study was made, and measurements could only be taken from a collection of scaled photographs. Since it was virtually impossible to take accurate chord measurements from these photographs, I have simply listed the shortest distance from head apex to vent in each case. On the other hand, the HLs may be considered reliable (even though based on photographs) since the head length measurement is not affected by uterine flexion.

3. Section Thickness (ST) and Plane of Sectioning (PS). Processed specimens were cut with a sliding microtome, usually at 10μ and in the frontal plane. While slow in operation, the quality of sections obtained with a sliding microtome is exceptionally good and consistent.

4. Stains. Specimens were generally fixed with Bouin's solution, although information on fixation was missing for some specimens. *L. catta* MPIH 1964/28 was fixed with 10% formalin. After decalcification, heads were imbedded, cut and stained. It will be noted that the specimens were stained by a variety of methods, many of which are not routinely used in comparative embryology. The reason for this is that most of the sectioned specimens described in this study were not originally intended for the type of analysis presented here. The majority of them were processed for use in neurological studies, using stains appropriate for that purpose (e.g., Cresyl Violet, Gabe, Klüver-Barrera). Unfortunately, such stains do not always provide superior visualization of specialized connective tissues. However, in this type of study the only tissues which must be sharply discriminated are bone and cartilage, and staining was usually adequate for this.

Prenatal specimens were invariably listed as "embryos" in the catalogues. However, since I selected for study those specimens which were in the late stages of uterine life, I prefer the term "fetus" as being more descriptive of their degree of development.

Specimens are listed in the tables as "near-term fetus", "newborn", "young infant", etc., only when this was specifically stated in the catalogues, or could be reasonably deduced from the state of development or ontogenetic data in published sources.

Since it was intended to study the development of otic structures through as many stages as possible, macerated adult skulls were also used. These materials are briefly listed in the Specimens sections of tables 2-1 to 7-1.

1.2.2 TAXONOMIC IDENTIFICATIONS

For ready reference, the taxonomic locations of the sectioned specimens are noted in table 1-1 (figures in parentheses give the number of sectioned specimens investigated in each taxon). Although the primary purpose of this dissertation is not to revise current classifications or to suggest new ones, a few notes on the taxonomy of the forms described here are desirable.

Specimens were distributed among four orders. I have followed modern opinion (e.g., MCKENNA 1966; CAMPBELL 1966; MARTIN 1968b; SZALAY 1968) in separating tree shrews from primates and in placing them within their own order, Tupaioidea. I have also followed PATTERSON (1965) and others in recognizing a separate order for elephant shrews (Macroscelidea), and MCDOWELL (1958) and others in placing all recent hedgehog-like and shrew-like small mammals in a single order (Lipotyphla). This is, quite purposefully, a conservative scheme; however, groupings above the level of order have been attempted (most recently by MCKENNA 1975). MCKENNA

Table 1-1

SYNOPTIC TABLE OF SECTIONED SPECIMENS

ORDER: PRIMATES (13) [primates]		
Grade: Strepsirhini (13) [strepsirhine prosimians]		
Infraorder: Lemuriformes (6) [lemurs]		
Family: Lemuridae (1) [true lemurs]	1	Lemur catta [ring-tailed lemur]
Subfamily: Lemurinae (1) [common lemurs]		
Subfamily: Lepilemurinae (0) [sportive lemurs]		
Family: Cheirogaleidae (4) [dwarf & mouse lemurs]	4	Microcebus murinus [mouse lemur]
Family: Indriidae (1) [indris & sifakas]	1	Propithecus sp. [sifaka]
Family: Daubentoniidae (0) [aye-aye]		
Infraorder: Lorisiformes (7) [lorises & galagos]		
Family: Lorisidae		
Subfamily: Lorisinae (1) [lorises]	1	Loris tardigradus [slender loris]
Subfamily: Galaginae (6) [galagos]	4 2	Galago (Galagoides) demidovii [dwarf galago] Galago (Galago) senegalensis [Senegalese galago]
Grade: Haplorhini (0) [tarsius & anthropoids]		
ORDER: TUPAIOIDEA (5) [tree shrews]		
Family: Tupaiidae		
Subfamily: Tupaiinae (5) [common tree shrews]	5	Tupaia (Tupaia) glis [common tree shrew]
Subfamily: Ptilocercinae (0) [pen-tailed tree shrews]		
ORDER: MACROSCELIDEA (2) [elephant shrews]		
Family: Macroscelididae (2)		
Subfamily: Macroscelidinae (2) [small elephant shrews]	2	Elephantulus fuscipes [Congolese long-eared elephant shrew]
Subfamily: Rhynchocyoninae (0) [large elephant shrews]		
ORDER: LIPOTYPHLA (10) [lipotyphlous insectivores]		
Suborder: Erinaceomorpha (4)		
Family: Erinaceidae (4) [hedgehogs]		
Subfamily: Echinosoricinae (0) [gymnures]		
Subfamily: Erinaceinae (4) [common hedgehogs]	4	Erinaceus europaeus [European hedgehog]
Family: Talpidae (0) [moles & desmans]		
Suborder: Soricomorpha (6)		
Superfamily: Soricoidea (1)		
Family: Soricidae (0) [shrews]		
Family: Solenodontidae (1) [solenodons]	1	Solenodon sp. [solenodon]
Superfamily: Tenrecoidea (5)		
Family: Tenrecidae (5) [tenrecs]		
Subfamily: Potamogalinae (0) [otter shrews]		
Subfamily: Oryzorictinae (1) [rice tenrecs]	1	Microgale (Nesogale) dobsoni [Dobson's long-tailed tenrec]
Subfamily: Tenrecinae (4) [common tenrecs]	3 1	Hemicentetes semispinosus [streaked tenrec] Setifer setosus [large Madagascan 'hedgehog']
Family: Chrysochloridae (0) [golden moles]		

places Primates and Tupaioidea (=Scandentia) within the grandorder Archonta, which also contains Dermoptera and Chiroptera. I do not know how valid a grouping Archonta is, although it receives some support from antigenic specificities of proteins (GOODMAN 1975; Chiroptera, however, are excluded). He also places Macroscelidea together with Lagomorpha in the grandorder Anagalida, and separates this taxon from the others considered here at the magnordinal level. There is certainly no longer any adequate support for the view that elephant shrews and tree shrews have special affinities.

With respect to taxon names and groupings beneath the ordinal and above the generic levels, I have taken the following actions. In the case of Primates, evidence is building (see CHARLES-DOMINIQUE and MARTIN 1970; GROVES 1974; DENE, GOODMAN, PRYCHODKO and MOORE 1976) that the lorises and lemurs are more closely related than was once thought. This should be reflected in some fashion in classification, and I have chosen to follow HILL (1953) in dividing the primates into the grades Stepsirhini (lemurs and lorises) and Haplorhini (Tarsius and anthropoids). I am not convinced that the basis for Haplorhini is so sound as that for Strepsirhini, although it too receives support from immunological data (GOODMAN 1975) and placental characters (LUCKETT 1974). However, since I present no new basicranial data on the former grade here, I accept HILL's concept without further comment (see also SZALAY 1976).

Strepsirhine higher taxa are in a state of flux at this point, and widely varying schemes of relationships have been suggested by recent authorities. The most drastic revision is that proposed by TATTERSALL and SCHWARTZ (1974) which, among other things, places cheirogaleid lemurs among the Lorisiformes. In older classifications (e.g., FIEDLER 1956) dwarf lemurs are regarded as no more than a subfamily of Lemuridae. In my view, so strong a lorisiform tie is not supported by the balance of taxonomic characters or by protein data, although it is probably no longer useful to claim that the differences between true and dwarf lemurs merit only a subfamilial separation. Accordingly, I join CARTMILL(1975) and others in recognizing a family Cheirogaleidae, but as a member of Lemuriformes.

Tree shrews seem to present few difficulties at ranks beneath that of the order. LYON's (1913) subfamilial separation of Ptilocercus from other tree shrews has not suffered any important challenges in recent years, although the extremely rare pentailed tree shrew has apparently not yet been studied by biochemical techniques. This may be significant, for GOODMAN (1975) has found that the average antigenic distance of Rhynchocyon from other macroscelideans is sufficient to warrant superfamilial separation. However, not all macroscelideans have been studied biochemically either, and PATTERSON's (1965) subfamilies are provisionally retained here.

Any attempt at groupings within Lipotyphla is riddled with problems; this order is historically one of the least stable in Mammalia. Although there are several competing schemes (e.g., SABAN 1954; VAN VALEN 1967; BUTLER 1972), each with its good points and deficiencies, I choose to follow MCDOWELL's (1958) concepts of within-group relations and taxon boundaries. It is quite possible that golden moles deserve their own order; perhaps, also, tenrecs should be raised to a rank co-ordinate with Erinaceomorpha and Soricomorpha. Yet promotions in rank do not make me more confident that we are really any closer to solving the geometry of relationships within the insectivore dustbin, and consequently I have taken a conservative course in the portrayal of lipotyphlan relationships.

Virtually all sectioned specimens were collected from the uteri or litters of wild-shot or zoo females. The generic and specific identifications of the females were made by experienced taxonomists, and the designations in the tables are reliable. All names were checked against the lists in NAPIER and NAPIER (1967) for strepsirhines and tree shrews, ELLERMAN, MORRISON-SCOTT and HAYMAN (1953) for African lipotyphlans, and CORBET and HANKS (1968) for elephant shrews.

Relevant common names which are not merely anglicized versions of taxon names (e.g., cheirogaleids) are also presented in table 1-1. When it is desirable to refer to lorises and lemurs as a group I use the term "strepsirhine prosimians" instead of "prosimians" alone in order to avoid any possible ambiguity. "Lipotyphlans" and "lipotyphlous insectivores" refer only to the forms included in the order Lipotyphla by MCDOWELL (1958). The common names for species were generally taken from NAPIER and NAPIER (1967; primates and tree shrews) and WALKER, et al. (1964; elephant shrews and lipotyphlans).

1.3 METHOD OF DESCRIPTION

In the absence of a useful model for the integrated description of the structures considered here, I have formulated my own. Each chapter in Part I is devoted to a separate taxonomic group, and descriptions are provided within a consistent, structure-by-structure framework. While a topical approach permits easy access to desired information and facilitates the comparison of descriptions by the user, it introduces a certain choppiness at the same time. In order to ease the reader's labour in this regard, I have assembled a general guide to some functional aspects of the middle ear and a comprehensive list of definitions. These appear in appendices I and II respectively. In addition, section 1.4 furnishes a systematic overview of the basic relations and development of all structures in the order in which they are discussed in each chapter.

A method of description or agenda is included at the start of each descriptive chapter. The organizational divisions of the agenda are self-evident and require only brief introduction. The first and second divisions list the bones, cartilages, outgrowths, and other features in the order in which they are discussed in the text. These are arbitrarily divided into structures found in the ventral and in the dorsal walls of the middle ear. This format appeared to me to be the most effective way of presenting my findings, although the user will be forced to go to both sections for details on bones which are involved in the formation of both the roof and sidewalls of the tympanic cavity.

The third division is concerned with the pneumatization of the middle ear and the septa which commonly subdivide it. The effects of pneumatization produce startling transformations of the middle ear in some groups, such as lorises. In other groups its effects are less profound, but are discussed nonetheless in the interests of completeness.

The final division incorporates observations on important soft tissues of the middle ear. However, descriptions are generally microanatomical *per se*, since most aspects of their development (except growth to definitive size) are completed before late fetal life. Chief attention is paid to the tympanic branchings of the internal carotid, since they have recognized taxonomic valency. The data on nerves and muscles are rather repetitious, since the forms employed here show little variation at the gross level. However, inclusion is warranted since there are several misunderstandings in the literature regarding their positions and relations.

Each structure selected for treatment was examined in the available series of sectioned and (for bony features) macerated specimens. Where appropriate, close studies of the histological characteristics of certain tissues were made during the microscopic examination of sections. By comparing sectioned with intact material it was possible to reconstruct the sequence of development and fate of many structures hitherto badly known. The large number of illustrations included in each descriptive chapter should enable the reader to visualize for himself the major steps in their ontogenetic transformation.

As a further aid to study, the auditory regions of several sectioned specimens were reconstructed according to the graphical point-plot method (PUSEY 1939; see also GAUNT 1971). This method has the advantages of ease and speed of execution, although the resulting depictions are less useful than the three-dimensional models achieved with wax plates and other media.

1.4 SYSTEMATIC OVERVIEW OF DESCRIBED STRUCTURES

This section explores, in précis form, the chief relations and development of the structures selected for description in the text. Short definitions for these structures are included in appendix II and will not be repeated here. Further information and an abundance of comparative examples may be found in the monographs of VAN KAMPEN (1905) and VAN DER KLAAUW (1931).

The order of presentation closely parellels that of the methods of description described earlier (see 1.3).

1.4.1 VENTRAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

I have separately defined "cavum tympani" and "presumptive tympanic cavity" in appendix II (q.v.) in order to make certain structural relationships unambiguous. The cavum tympani is properly the air filled space,[1] bounded by an entodermal membrane, which derives from the first (and possibly the second) phayngeal pouch (cf. BAST and ANSON 1949:306-307). It is situated within the presumptive tympanic cavity, the bony or partly-membranous chamber on the underside of the skull. In the adult the one entirely fills the other, and there is usually no reason to discriminate them anatomically (especially in macerated material). However, they are not co-extensive in earlier phases of ontogeny and the usage of adult morphology is therefore not acceptable. In this study, "ventral wall of the tympanic cavity" (or middle ear) should always be understood to mean "of the presumptive tympanic cavity" unless specifically stated otherwise.

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[1] In post-natal life; in the fetus, the cavum tympani is filled with amniotic fluid.

With this distinction in mind, we may turn to the structures which form the (presumptive) ventral wall. The first of these to develop is the fibrous membrane, a feature which is worth describing in detail here because its significance has not been previously understood.

1.4.1.1 Fibrous Membrane of the Tympanic Cavity

The fibrous membrane appeared in all species used in this study which were represented by sufficiently early stages. Its development and relations to other structures show certain regularities of extreme importance.

As the mesenchyme surrounding the cavum tympani begins to loosen and assume a myxomatous form, a definite membranous boundary appears between the tissue destined to become the tympanic mucoid tissue and the tissues ventral to it. This boundary, the nascent fibrous membrane, is chiefly distinguishable from other tissues in its immediate area by its sheet-like form and high fiber content. With further differentiation, the membrane generally becomes much denser as the number of fibers increases, although there is variation in this among species. The definitive membrane resembles, and is partially continuous with, other dense connective tissues covering the basicranium.

The disposition of the fibrous membrane is much the same in all specimens, and special characteristics in individual species will be treated in the appropriate chapters. In the typical case (fig. IV-7), dense connective tissues (chiefly perichondria and fasciae) closely invest the underside of the central stem and the medial wall of the pars cochlearis. A separate sheet (now identifiable as the fibrous membrane) separates from the rest, passes down the medioventral side of the presumptive tympanic cavity, then beneath the ectotympanic and finally upwards towards the perichondrium of the auricular cartilage. In cross-sections the membrane appears as a dark-staining, semicircular band which completely isolates the presumptive tympanic cavity from structures lying around it. As is apparent from the figure, the fibrous membrane has no connection with the pars tensa of the tympanic membrane.

Considered three-dimensionally, the fibrous membrane is shaped like an irregular hemisphere which ventrally cloaks the entire presumptive tympanic cavity. It is usually somewhat diffuse near the anterior end of the cavity and well-developed in its middle and posterior portions. The presumptive tympanic cavity ends behind the fossula fenestrae cochleae, and the fibrous membrane here blends with the dense connective tissues covering the posterior part of the auditory capsule. It is punctuated at intervals by vessels, nerves and other structures which enter the presumptive tympanic cavity between the ectotympanic and the ventral surface of pars cochlearis (e.g., internal carotid artery, cartilage of the auditory tube).

The fibrous membrane of the tympanic cavity is highly significant for several reasons. First, its existence denies the sharp distinction sometimes made between bony and membranous methods of ventral enclosure of the tympanic cavity. During ontogeny, the fibrous membrane appears well before, and whether or not, tympanic processes are formed. In species which develop complete bullae, the fibrous membrane is functionally replaced by the latter; it remains, however, as the external covering of the bullar periosteum. In species which do not develop complete bullae, the fibrous membrane continues to separate the air-filled spaces of the middle ear from surrounding soft tissues. Further, there is no reason to agree with VAN DER KLAAUW (1931:18) that cases of unossified ventral walls in fossils suggest that unattached or cartilaginous entotympanics were originally present, but fell away after death. It is far more probable that the ventral wall was truly membranous, i.e., composed of the fibrous membrane alone throughout ontogeny.

Secondly, the fibrous membrane performs an important function related to the growth of the various tympanic processes or independent elements (entotympanics) which may appear in the ventral wall later in ontogeny. Tympanic processes, when they begin to develop, are not randomly oriented with respect to the fibrous membrane, but arise immediately adjacent to it. Further, the trajectory of their growth appears to be at least initially conditioned by the disposition of the fibrous membrane. The membrane seems to act as a scaffolding or framework along which the processes grow ventrally in much the same way that the intramembranous bones of the vault grow along the ectomeninx. This is most clearly seen in the method of growth of the petrosal plate in fetal strepsirhines. Naturally, the adult bulla does not reproduce the original radius of curvature of the fibrous membrane because the former swells enormously during ontogeny as a result of pneumatization.

The growth of the entotympanics is even more interesting in this regard. Unlike tympanic processes (which are merely outgrowths of basicranial bones), the anlagen of entotympanics actually differentiate within the fibrous membrane instead of adjacent to it. This has an undeniable influence on their pattern of growth. Also, the method of development of the entotympanics suggests that they have an utterly different history than the other bones of the auditory region (see 8.5).

There are few references to the fibrous membrane in the published literature. BAST and ANSON (1949) describe the loosening of the mesenchyme within the presumptive tympanic cavity and its conversion into a mucoid tissue, but fail to mention the concurrent production of the fibrous membrane. It is, however, clearly present in a human fetus of 16 weeks illustrated by these authors (1949:308, fig. 132C; see also ANSON and DONALDSON 1973:26, fig. II-5). The only detailed reference I have found appears in FRICK's (1954:69-71) study of cranial development in the vespertilionid bat *Myotis myotis*. "Fibrous membrane" is a free translation of his term for the same structure (*Bindegewebshuelle*).

1.4.1.2 Cartilage of the Auditory Tube

The cartilage of the auditory tube is a constant feature of the anterior end of the auditory region. However, little is known about its development or structural variability since most accounts of mammalian auditory regions are based on macerated rather than fresh or sectioned materials.

In addition to providing brief descriptions of the form and relations of the tubal cartilage for each of the groups of interest here, my major purpose in studying this element was to collect data for a re-analysis of its obscure relationship with the (rostral) entotympanic (see 1.4.1.3 and 8.5.2). In some forms, the rostral entotympanic arises from its own anlage and never displays an intimate association with the cartilage of the tube. In others, it appears to develop as a direct outgrowth of the tubal cartilage, while in still others the two arise separately but later fuse. The second and third situations occur in *Tupaia* (SPATZ 1966; this study) and elephant shrews (VAN DER KLAAUW 1931; this study), while the first is known to happen in several unrelated mammals (VAN DER KLAAUW 1931). I found no clear evidence of primary or secondary fusion of a rostral entotympanic with the tubal cartilage in either strepsirhine prosimians or lipotyphlans, and it is now virtually certain that the rostral entotympanic never forms during the ontogeny of modern primates and insectivores (but see 8.5.4). Previous studies established only that a free (rostral) entotympanic was absent in adult stages of these groups.

I had hoped to be able to clarify one other important aspect of the development of the cartilage of the tube, its ontogenetic origin. Widely varying opinions exist regarding its method of formation. KEIBEL (1912:282) states (for *Homo*) that the tubal cartilage has no relationship to the visceral skeleton, but is an independent formation. FAWCETT (1919) infers that it arises from the tissues of the first pharyngeal pouch, while BAXTER (1953:243) believes that it may be a derivative of the third arch. Unfortunately, I cannot securely choose among these alternatives since my sectioned specimens were too advanced in age. However, all sources agree that the tubal cartilage arises comparatively late in ontogeny, long after the appearance of those cartilages which definitely arise from visceral bars (e.g., Meckel's, Reichert's).

At present, no proof of the material continuity of tubal cartilage and visceral skeleton exists, and it is clearly an excess of refinement to claim that the cartilage arises from a specific part of the viscerocranium. Accordingly, I treat the cartilage of the auditory tube as a structure *sui generis*.

1.4.1.3 Bones of the Basicranium: Tympanic Processes and Other Structures

The next set of descriptions report the development and relations of the plates of bone which border the presumptive tympanic cavity. These plates are usually outgrowths of the constant bones of the basicranium (e.g., tympanic process of the basisphenoid); in a few cases independent ossifications (traditionally referred to as entotympanics) which are not universal among mammals form part of the floor of the middle ear.

As is well known, the form and composition of the ventral wall vary considerably. However, there is usually a high degree of consistency within major groups, and the construction of the ventral wall often figures prominently in definitions of mammalian higher taxa.

VAN DER KLAAUW's (1931:233) comprehensive list of elements which may lie in the ventral wall includes: the ectotympanic, petrosal, squamosal, alisphenoid, basisphenoid, entotympanic, pterygoid, basioccipital, exoccipital, gonial, accessory malleolar ossicles, element of Spence and tympanohyal. Of these, the basioccipital and exoccipital do not occur in the ventral wall in the forms described here (although they do in a few other mammals). Further, the last four elements are of minor interest and receive no more than cursory treatment. The gonial is a constant ossification which is perhaps equivalent to the reptilian prearticular (DE BEER 1937); it normally fuses with the head of the malleus to form the processus gracilis and is a bullar component only to the extent that it projects into the Glaserian fissure. Accessory ossicles are inconstant, and I found no instance of such independent ossifications in the sectioned specimens. The element of Spence (and the element of Paaw) are likewise inconstant; they are briefly described, where they occur, in relation to their soft-tissue connexions (chorda tympani and stapedius muscle, respectively). The tympanohyal, an ossification appearing within the material of the second visceral bar, is treated in conjunction with Reichert's cartilage and the structures of the dorsal wall (see 1.4.2.1).

The remaining members of VAN DER KLAAUW's list are given full treatment under the following headings:

- Tympanic Processes of the Petrosal
    - Rostral tympanic process
    - Caudal tympanic process
- Ectotympanic
- Tympanic Process of the Basisphenoid
    - Pterygoid
- Entoglenoid Process of the Squamosal
- Tympanic Process of the Alisphenoid
- Entotympanics
    - Rostral entotympanic
    - Caudal entotympanic

(1) Tympanic Processes of the Petrosal

Although VAN DER KLAAUW (1931) seemingly felt that a legitimate distinction could be made between tympanic processes arising from 'pars petrosa' (i.e., pars cochlearis) and from 'pars mastoidea' (i.e., pars canalicularis), his grounds for making the distinction were never clearly stated and no later author has attempted to clarify the matter. Ontogenetic investigations of modern mammals confirm not only that VAN DER KLAAUW's distinction is valid, but also that the distribution of tympanic processes of the petrosal among mammals is much wider than is usually thought.

Following VAN DER KLAAUW's terminology, I distinguish here rostral and caudal tympanic processes of the petrosal (hereafter, RTPP and CTPP). While ontogeny shows that there is a high degree of uniformity in their sites of origin, a certain amount of variation and the effects of later development mask the regularities which do occur. Fig. I-2 schematically depicts the auditory region of a hypothetical fetal mammal in the ventral aspect. On the basis of findings presented in the text, I conclude that tympanic processes, when formed, tend to arise within two circumscribed zones on the underside of the auditory capsule. The first, for the RTPP, stretches from the anterior pole of the promontory to the region of the processus recessus, along the middle portion of the pars cochlearis. The second, for the CTPP, arcs mediolaterally across the anteroventral portion of pars canalicularis, from the region of the processus recessus to the position of the foramen stylomastoideum (primitivum).

Of the two processes, the RTPP has the narrower distribution and requires only a brief introduction. It is an intramembranous or periosteal outgrowth of the pars cochlearis, and only begins to develop once the underside of this part of the auditory capsule is ossified. In some forms (e.g., strepsirhines, elephant shrews), the RTPP arises from the entire length of the zone apportioned to it in fig. I-2. In others (e.g., Erinaceus), the RTPP is restricted to a part of this zone and never attains large size. Extreme pneumatization of the middle ear during postnatal life may result in the 'migration' of the RTPP to a more medial position (e.g., in strepsirhines), but it always appears first within the zone indicated in fig. I-2.

There is no ontogenetic evidence for the position that the RTPP of primates is an entotympanic which has lost its independence and now appears as an outgrowth of the petrosal (see 8.5.5).

A number of ridges and processes spring from the hind part of the auditory capsule in different mammals. However, the sample of sectioned specimens indicates to me that there is a fairly restricted zone which gives rise to true tympanic processes, i.e., outgrowths which adjoin the fibrous membrane of the tympanic cavity.

It is first necessary to specify the zone for the CTPP in relation to other otic features. Directly behind the apertura fossulae fenestrae cochleae (fig. I-1) is a small fossa or pit (D_3, fig. I-2) which accommodates the saccus posterior of the cavum tympani during life. Lateral to this fossa is another small depression which lodges the origin of the stapedius muscle (SF, fig. I-2). The fibrous membrane of the tympanic cavity meets the auditory capsule along an arc which runs from the medial wall of the apertura fossulae fenestrae rotundae, then behind D_3, to the stapedius fossa. This arc closely corresponds to the zone in which the CTPP appears during ontogeny.

However, it is not uncommon to have only part of this zone involved in the production of the CTPP. This, combined with the fact that the CTPP has a more complicated ontogeny than the RTPP, makes general description difficult. In order to promote regularity in text descriptions I subdivide the zone producing the CTPP into three morphological sections (medial, posterior and lateral). The medial section arises from the MWF, which is the ossified successor of the processus recessus (see appendix II). The MWF is always raised to some degree from the general plane of the dorsal wall of the tympanic cavity, but it is not always built into a prominent ridge. It is therefore difficult in some cases to separate the medial section of the CTPP from the MWF per se. However, the MWF is a universal feature of eutherians, and it is really a matter of nomenclature rather than concept whether it is regarded as part of the CTPP. In any event, I point out in the text cases where it is not useful or informative to recognize a definite medial section.

Another ridge, the posterior section of the CTPP, is commonly formed lateral to the medial section. These two sections are usually more or less inseparable by late fetal life, but the posterior section deserves a separate label since it is not part of the true processes recessus (or MWF).

Most references to posterior tympanic processes of the petrosal take note of the coalesced medial and posterior sections; however, there is also a lateral section which rarely receives attention.

The lateral section arises in one of two main positions. In some cases (e.g., Tupaia), a pronounced ridge appears alongside the medial border of the fossa for the stapedius muscle. Because this ridge (5c', fig. I-2) strikes anteriorly, it seems to enter the tympanic cavity rather than bound it. However, this is not the true situation; in mammals to which this description is applicable, the fibrous membrane of the tympanic cavity stretches between this ridge and the base of Reichert's cartilage (or tympanohyal, in the case of the adult). The origin of the stapedial muscle is thus rendered extratympanic in position, and the belly of this muscle must pass through the membrane-filled gap between the ridge and Reichert's cartilage in order to insert upon the stapes. Accordingly, it is accurate to regard the ridge as the true posterolateral boundary of the tympanic cavity, despite its misleading position.

In other cases (only lorises and lemurs among the forms studied here), the ridge mentioned above is absent. Instead, a wholly different structure, the posterior continuation of the crista parotica (fig. I-1) is responsible for the production of the lateral section of the CTPP. In fetal mammals the posterior continuation of the crista parotica is usually no more than a low eminence behind the base of Reichert's cartilage. Further, in most of the species investigated here, the posterior continuation does not become involved in the bounding of the tympanic cavity, but instead lies outside of it according to the disposition of the fibrous membrane. In strepsirhines, however, the fibrous membrane attaches to the auditory capsule along the arc 5a - 5b - 5c" (fig. I-2). Further, section 5c" enlarges considerably, and, as a consequence, renders the origin of the stapedius muscle intratympanic in position.

I am conscious of the fact that the division of the CTPP into sections may imply to some that this process is not homologous in different mammals. However, the chief difference between groups is in size, not in disposition. Medial, posterior and lateral sections, if all are formed, generally arise at nearly the same time and form a more or less continuous ridge early in ontogeny. The only fundamental difference in construction relates to whether the posterior continuation of the crista parotica is involved, and this appears to be a specialization of strepsirhines.

Unlike the RTPP, the CTPP arises in cartilage first and is later ossified by centers within the auditory capsule. Its degree of growth and pneumatization is usually small, although it occasionally reaches large size (e.g., Microgale). In cases where it does grow significantly, it may articulate with the posterior crus of the ectotympanic (e.g., Solenodon) or meet the tympanohyal (e.g., Erinaceus). There is no ontogenetic evidence that the CTPP is a suppressed entotympanic.

Although the CTPP arises in the area traditionally (and loosely) called the mastoid, it is preferable to avoid calling it a 'mastoid process' (cf., however, STARCK 1962) because of the terminological chaos surrounding the latter term. The CTPP is clearly not the homologue of the human mastoid process (VAN KAMPEN 1905), and it does not provide origins for muscles in any event.

A final note is required regarding the usage of the term 'petrosal plate'. The RTPP and CTPP, if both are formed and develop to some degree, often grow together or coalesce in order to form a single process. It is useful to have a separate term to refer to the conjoined RTPP and CTPP, and 'petrosal plate' (first used by VAN DER KLAAUW 1931) has a self-evident reference.

(2) Ectotympanic

The ectotympanic is a constant bone of the mammalian basicranium and always arises intramembranously. During fetal life it originates (sometimes from multiple centers) as a narrow horsewhoe around the developing tympanic membrane. During later ontogeny, embryonic proportions may be retained (as in modern lemurs and tree shrews), although the bone of course increases in diameter. Far more commonly, the ectotympanic eventually develops medial or lateral outgrowths from its periphery and is consequently described as 'expanded'. A relatively unexpanded ectotympanic has traditionally been regarded as the ancient mammalian condition (VAN KAMPEN 1905; GREGORY 1910; VAN DER KLAAUW 1931; but see SZALAY 1975), although cases in which expansion is completely absent are very rare. Extreme medial expansion, resulting in the formation of a complete ectotympanic bulla, is characteristic of a few groups, such as the rodents. A slight degree of medial outgrowth, however, is quite common. Similarly, a moderate degree of lateral expansion is nearly general among mammals. Marked growth of the lateral periphery can produce a cylindrical or semi-cylindrical aperture, the so-called bony external acoustic meatus.

Medial and lateral expansions of the ectotympanic, as well as other structural features, often figure prominently in taxonomic studies. Their gross ontogeny, however, is rather simple and I can offer little insight into why they are present in some forms but absent in others. Since the structural variety of the ectotympanic among adults of the groups discussed here is well known, I have generally limited description to the most pertinent details of ectotympanic development.

The topographical relationship of the ectotympanic to other elements of the ventral wall often receives detailed treatment in the literature. Usually, the relationship is described only in terms of its appearance in the (adult) macerated skull: does the ectotympanic simply abut, fuse with, or lie under cover of some other component of the ventral wall? There are virtually no detailed descriptions of how these relationships develop, nor any analysis of the highly significant role played by surrounding soft tissues. Accordingly, I devote a separate section to the ontogeny of relationships in each descriptive chapter (see also 8.1.5).

It has been necessary to introduce some new terms in order to describe the various relationships of the ectotympanic. In paleoprimatology it is conventional to use the familar dyad "extrabullar" and "intrabullar" when describing the situation of the ectotympanic, but these terms have objectionable connotations. The ectotympanic and its major associated structure, the tympanic membrane, always form the boundary between the middle and external ears. Consequently, it is illogical to speak of the ectotympanic as being "inside" or "outside" the bulla or tympanic cavity (see SIMONS 1974; CARTMILL 1975).

Since the traditional terms simply refer to whether or not the ectotympanic is visible from the ventral aspect, I recommend the following terms as replacements:

1. Phaneric ("seen", "visible"). Here used to describe the ectotympanic in cases in which it is exposed in the ventral wall of the tympanic cavity. Equivalent to "extrabullar", in the usual meaning of that term.

2. Aphaneric ("not seen", "not visible"). Here used to describe the ectotympanic in cases in which it is occluded by other components of the ventral wall. Equivalent to "intrabullar", in the usual meaning of that term.

These two conditions of the ectotympanic do not exhaust all possibilities, especially when mammals other than primates are considered. Accordingly, I also recommend the adoption of these terms:

3. Semiphaneric ("partly seen", "partly visible"). Here used to describe the ectotympanic in cases where it is only slightly covered by other components of the ventral wall.

4. Athictic ("not touching"). Here used to describe the situation in which the ectotympanic and some other component are separated by an appreciable gap.

These terms, like their predecessors, should be used to describe the predominant picture in any given instance. For example, the condition of the ectotympanic in lemurs is predominantly an aphaneric one, in that the petrosal plate entirely covers that bone except for a small part of its posterior crus.

One advantage of these terms is that they can be used in combination in instances where a complex of bones take part in the construction of the ventral wall. For example, in Erinaceus the ectotympanic is semiphaneric with respect to the tympanic process of the basisphenoid, but athictic with respect to the caudal tympanic process of the petrosal.

A final, minor subject of interest is the rotation of the ectotympanic during ontogeny. As seen in cross-sections, the angle between the horizontal plane and the plane of the ectotympanic often alters markedly between fetus and adult. In young stages of mammals, the angle is at first quite small and the ectotympanic is highly inclined. During later phases of development, the angle usually increases and the ectotympanic assumes a more upright position. However, there is wide variation among adult mammals in the actual degree of ectotympanic rotation. In part, this variation is related to differences in brain size and the expansion of the neurocranium. Also significant is the size of tympanic processes and whether or not they modify the position of the ectotympanic as they grow (see FORSTER 1925). In the descriptive chapters, values for the inclination angle are listed in tables and compared with known adult measurements from the literature.

(3) Tympanic Process of the Basisphenoid

The tympanic process of the basisphenoid, when present, arises from the margins of the basisphenoid close to the junction of the latter with the auditory capsule (fig. I-2). It originates as a periosteal outgrowth in all the forms studied here which possess it. Like the tympanic processes of the petrosal, it develops adjacent to the fibrous membrane of the tympanic cavity.

During ontogeny, the tympanic process of the basisphenoid flares posteriorly and ventrally, often to a pronounced degree. Accordingly, even though it initially arises in the extreme anteromedial corner of the tympanic cavity, in the adult this process may broadly articulate with the greater part of the medial side of the promontory as well as the ectotympanic (e.g., Erinaceus; see figs. VI-1, VI-2). Since the tympanic process of the basisphenoid medially borders the foramen caroticum primitivum from the start (fig. I-1, I-2), the anterior carotid foramen of the adult is always situated within the confines of the tympanic cavity (see 1.4.2) in species possessing this outgrowth.

VAN DER KLAAUW (1931:245) notes that a tympanic process of the basisphenoid seems to be limited to certain insectivores. This view may still be taken as broadly accurate, although I disagree with him that the process is entirely lacking in Macroscelidea. Among the living Lipotyphla, the process is well-defined in erinaceomorphs and tenrecoids, but is curiously absent (or perhaps vestigial, in MCDOWELL's 1958 view) in soricoids. It is absent in primates and tree shrews.

The posterior part of the pterygoid bone sometimes participates in the formation of the bony ventral wall, although its contribution is usually overlooked because the bone completely fuses with the basisphenoid and alisphenoid during ontogeny.

Material derived from the pterygoid occupies the 'angle' of the anteromedial extremity of the tympanic cavity, where the tympanic processes of the basisphenoid and alisphenoid meet one another in lipotyphlans (e.g., *E. europaeus*; see fig. VI-1). Accordingly, it is really a matter of anatomical convenience whether the pterygoidal contribution is considered part of the one or the other process. In the text, the pterygoid is usually discussed in conjunction with the tympanic process of the alisphenoid.

(4) Entoglenoid Process of the Squamosal

The entoglenoid area of the squamosal sometimes directly bounds the anterolateral portion of the tympanic cavity (as defined by the fibrous membrane). Its ontogeny is somewhat difficult to trace in young specimens, since the entoglenoid process (if formed) characteristically develops rather late (see VAN DER KLAAUW 1929). It is not, for example, sharply distinguishable from the rest of the squamosal in young tenrecs, even though the process is large in the adult stage of these mammals. On the other hand, I have found nothing unusual in its development in the specimens and stages available to me. Like most other tympanic processes, it is simply a periosteal outgrowth of its parent bone.

I have attempted to follow MCDOWELL's (1958) discrimination between the entoglenoid process and the true processus postglenoideus as far as possible. The basis for this distinction is covered under the appropriate headings in appendix II.

(5) Tympanic Process of the Alisphenoid

The tympanic process of the alisphenoid is here regarded as any outgrowth arising from the rear of the alisphenoid that bounds the anterior end of the tympanic cavity (see fig. I-2). Further, it is regarded as present in lipotyphlans, macroscelideans, and the tupaioid genus Ptilocercus, and as absent or vestigial in strepsirhines and tupaiines. I do not know whether the process is homologous in all the forms considered to possess it, but homology is likely on the basis of what is known about its ontogeny.

I have avoided using MCDOWELL's (1958:127) term "preotic crest" for the alisphenoidal outgrowth of insectivores since it carries the unnecesssary (and unproven) implication that this structure is not the homologue of similar structures occupying similar positions in other mammals. The preotic crest is simply a tympanic process of the alisphenoid which does not meet the ectotympanic--an unimportant distinction at best. Tympanic outgrowths vary considerably in their relationships with the ectotympanic, even within families. Nor is a close relationship between the ectotympanic and the tympanic process of the alisphenoid solely a marsupial character, which MCDOWELL also implies. It is found in elephant shrews, for example, and the two nearly meet in Ptilocercus.

In fig. I-2, the tympanic process of the alisphenoid is shown as separate from the tympanic process of the basisphenoid and the pterygoid bone. In point of fact, all three can meet at the anteromedial extremity of the tympanic cavity, and in the adult it is normally impossible to distinguish them from one another at this location. Accordingly, even though traditional terminology will be retained in this instance, it is important to remember that the 'tympanic process of the alisphenoid' often consists of a small amount of basisphenoidal and pterygoidal material as well.

(6) The Entotympanics

Entotympanics occur in only two of the groups surveyed here--Tupaioidea and Macroscelidea. The ontogeny of these elements in tree shrews and elephant shrews has already been studied by SPATZ (1966) and VAN DER KLAAUW (1929), although I have a number of additional observations to add to their descriptions. It has long been suggested that entotympanics may occur in primates (e.g., GREGORY 1910; see also STARCK 1975); this study is the first to demonstrate with suitable material (i.e., sectioned young specimens) that this is not the case, at least for strepsirhines. They are also absent in lipotyphlans, as far as is known.

There is so much variation among mammals in the position of origin and other characteristics of the entotympanics that it is no simple matter to provide a brief introduction to them. Unlike the tympanic processes discussed previously, they have no primary connexion with the constant bones of the basicranium (although they may have varying relations with the cartilage of the tube and Reichert's cartilage). They are, at least initially, independent elements of the ventral wall of the tympanic cavity. What endows them with considerable interest is their apparent restriction to, and uneven distribution among, mammals.

Two entotympanics are normally discriminated, the rostral and the caudal (VAN DER KLAAUW 1922, 1931). The rostral entotympanic often, but not always, appears in close relation to the cartilage of the tube and is sometimes primordially continuous with it. The caudal entotympanic is more variable, but in the majority of cases it appears first in the rear of the ventral wall. It may grow only a little, or it may eventually extend between the ectotympanic and the petrosal. Both entotympanics usually arise in cartilage, but this too is variable. They cannot be considered especially uncommon in modern mammals, although they are apparently absent in many orders (notably primates).

Other details regarding these elements are presented in section 8.5, which is a comprehensive review of previous ontogenetic investigations of the entotympanics and theories of their origin.

(7) Other Features

Certain other features are best considered in relation to the development of the ventral wall. These include the linea semicircularis and 'anulus membrane', which are dealt with in the chapters on lemurs and tree shrews (chapters 2 and 4) and are defined in appendix II.

1.4.2 DORSAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

Under this heading the contributions of basicranial bones to the roof of the middle ear are defined and described. The composition of the dorsal wall is rather less variable than that of the ventral, yet it nonetheless exhibits great structural complexity and deserves closer study than it usually receives.

Any bony contribution to the dorsal wall is called an 'epitympanic wing' in this study.[1] The term 'tympanic process' is often employed in this context, but here that term is reserved for outgrowths participating in the ventral wall.

The format for description of the dorsal wall is similar to that of the ventral wall. In each chapter, a brief introduction relates epitympanic wings to one another as they appear in the adult, and includes notes on the placement of foramina and other apertures. This is followed by details of the ontogeny of individual wings. The promontory of the petrosal, of course, always forms part of the roof of the tympanic cavity; however, it is beyond the scope of this presentation to describe its growth and development.

1.4.2.1 Bones of the Basicranium: Epitympanic Wings and Other Structures

In the young fetus, the dorsal wall of the middle ear is rather narrow and mostly membranous. Later, the dimensions of this wall enlarge considerably, and surrounding bones send out epitympanic wings into the membranous area (known as the piriform fenestra). However, these sheets of bone do not always entirely cover the tympanic cavity. This is because the dimensions of the presumptive tympanic cavity are affected by the growth of the rest of the basicranium, especially the central stem. The auditory capsule always lies behind a transverse plane drawn through the basioccipital-basisphenoidal synchondrosis (fig. I-1). Since this synchondrosis is one of the major growth sites of the basicranium, it follows that the auditory capsule will suffer relative displacement backwards during ontogeny. Since the capsule itself does not increase significantly in size after ossification (BAST and ANSON 1949), it also follows that a very large dehiscence would exist in the adult mammal unless epitympanic wings were formed. In some forms (e.g., strepsirhines), the pace of growth of epitympanic wings during preadult ontogeny is sufficient to close over the piriform fenestra seen in the fetus, despite extensive concurrent growth at the synchondrosis. In other forms (especially soricids), however, the rate of growth of epitympanic wings falls behind that of the synchondrosis, resulting in the persistence of the piriform fenestra into adulthood (fig. VII-1).

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[1] The term 'tegmen tympani' is retained, however, because it is a familiar term and because 'epitympanic wing of the petrosal' is used to refer to another dorsal outgrowth of the petrosal.

Technically speaking, therefore, the piriform fenestra is never absent in young stages of mammals, although it may suffer obliteration in later ontogeny. For example, soricids do not differ from other placentals because they have independently acquired a piriform fenestra, but rather because they retain a universal condition of the fetal dorsal wall throughout ontogeny.

The growth of the dorsal wall is also of strong interest for another reason. Taxonomic characters are often based on the disposition of foramina for the tympanic branchings of the carotid system and for certain nerves travelling through the middle ear. However, it should be recognized that most of these foramina do not exist *ab initio*. In the fetus, virtually all of the vessels of systematic interest simply pass through the large piriform fenestra on their way to their respective destinations. Depending on which epitympanic wings grow the most, the exit points of these vessels may become isolated within one or another epitympanic outgrowth, or remain within a remnant part of the piriform fenestra. Although the placement of these foramina may vary considerably among adults of different species, they are all produced in essentially the same way. An understanding of this point permits a clearer interpretation of the actual variation of some apertures, principally the anterior carotid foramen (see appendix II).

The dorsal contributions of basicranial bones are considered under the following headings:

Tegmen Tympani
Epitympanic Wing of the Petrosal
  (Reichert's cartilage)

Epitympanic Wing of the Sphenoid

Epitympanic Wing of the Squamosal

Epitympanic Wing of the Entotympanic

(1) Tegmen Tympani, Epitympanic Wing of the Petrosal, and Reichert's Cartilage

The tegmen tympani is constant in Mammalia (DE BEER 1937), although it is not always well-developed. The tegmen tympani forms the posterolateral part of the roof in advance of the sulcus for the facial canal (fig. I-3). In primates it attains large size, while in lipotyphlans it typically remains small (SPATZ 1964). The tegmen tympani is also relatively large in tree shrews and elephant shrews, however, which shows that a large tegmen is not solely a primate character. It is initially a cartilaginous outgrowth, but often expands markedly in later growth through periosteal ossification.

The tegmen tympani is not the only petrosal outgrowth which may be found in the dorsal wall, contrary to popular belief. The anterior pole of the promontory often gives rise to a small plate, which I term the epitympanic wing of the petrosal (fig. I-3). This wing does not usually attain broad dimensions, but it is nonetheless distinct in forms which express it and deserves separate mention. It is always initially independent of the tegmen tympani, which forms more posteriorly, although the two may meet (and eventually fuse) during their period of growth. The epitympanic wing of the petrosal appears to be identical to the crista promontorii medioventralis described by MACINTYRE (1972:291) for ancient placentals, although the process is not necessarily limited to the medial side of the anterior pole in modern forms.

Reichert's cartilage, which is at first a completely independent entity, derives from the visceral bar of the hyoid arch. It always lies at the posteroexternal angle of the auditory capsule in close relation to the exit-point of the facial nerve (fig. I-1). Fairly early in ontogeny, this cartilage fuses with the crista parotica (from which the tegmen tympani springs). A variable number of ossification centers may appear in Reichert's cartilage; its dorsal part may be ossified by the petrosal in some cases.

I have not attempted to deal with the ontogeny of Reichert's cartilage (or the rest of the visceral skeleton), as this is adequately covered in specialized works (see especially CORSY 1933; SPRAGUE 1944). Its principal importance here is its relation to the entotympanic problem, since the caudal entotympanic is sometimes thought to arise from the material of the second arch. I do, however, note for the sectioned specimens whether tympanohyal and stylohyal centers are exhibited, and briefly discuss the disposition of Reichert's cartilage (or its ossified successor) to other tympanic features.

(2) Epitympanic Wing of the Sphenoid

I have titled this outgrowth the "epitympanic wing of the sphenoid" for the simple reason that both the alisphenoid and the basisphenoid may participate in its formation. Unfortunately, it is often quite difficult to separate the two parts of the sphenoid in adult skulls because these bones completely fuse.

However, in some cases only the alisphenoid forms this wing, and here it is appropriate to identify an epitympanic wing of alisphenoid. In order to explain why it is that some mammals display the basisphenoid within the roof of the tympanic cavity and others do not, it is necessary to return to some details of the growth of the basicranium.

It was noted in section 1.4.1 that the tympanic process of the basisphenoid (when formed) originates along the medial side of the foramen caroticum primitivum. Accordingly, at least part of the basisphenoid (i.e., the area immediately adjacent to the foramen; see fig. I-2) will necessarily appear in the dorsal wall, since the tympanic process of the basisphenoid bounds the tympanic cavity ventromedially. For this reason, it is legitimate to identify a basisphenoidal contribution to the epitympanic wing of the sphenoid in cases where the tympanic process of the basisphenoid is present (area 1a in fig. I-3).

However, when the tympanic process of the basisphenoid is not formed, the anterior carotid foramen (and therewith the whole of the basisphenoid) almost always lies outside the walls of the tympanic cavity. Exclusion of the basisphenoid occurs in strepsirhines, for example (fig. I-2), since their bullae are formed by tympanic processes of the petrosal which lie lateral to the position of the basisphenoid. It is hardly necessary to state that the basisphenoid enlarges during strepsirhine ontogeny, just as it does in lipotyphlan ontogeny. However, if the usage of 'epitympanic wing' is to have any meaning, it is necessary to disregard any bones or processes which do not actually take part in the construction of the dorsal wall, no matter what their degree of growth or enlargement.

(3) Epitympanic Wing of the Squamosal

The medial surface of the squamosal typically sends out a long, usually narrow shelf which medially articulates with the tegmen tympani (fig. I-3). This epitympanic wing generally forms the lateral part of the roof for the epitympanic recess.

(4) Epitympanic Wing of the Entotympanic

In tree shrews alone, the (?rostral) entotympanic achieves the roof of the tympanic cavity. The epitympanic part of the entotympanic, although large, is simply an extension of the body of the rest of the bone (which, of course, lies in the ventral wall). The curious thing is that this dorsal contribution grows beneath the well-developed epitympanic processes of other basicranial bones, forming a sort of 'second roof'. When the entotympanic is stripped away (fig. IV-4), the dorsal wall of tree shrews differs very little from that of lipotyphlans.

1.4.3 PRINCIPAL SPACES AND SEPTA OF THE MIDDLE EAR

This section covers the major cavities of the middle ear and the small ridges and partitions found within them. Both sets of features have assumed a minor significance as sources of taxonomic characters, which is the major reason for their inclusion here.

SABAN (1956-57, 1963, 1964) has already described, in great detail, the adult anatomy of the principal spaces and septa found in most of the mammals discussed here. As his notes can scarcely be improved upon, I have limited myself to short statements on the ontogeny of the more important cavities and ridges. His system of nomenclature is generally used in the following chapters. Disagreements between his findings and mine are briefly noted where relevant.

The middle ear of the adult mammal is topographically a single space, despite the complexity it achieves in certain species.

The agencies which produce the various chambers, pockets and spaces of the middle ear are usually lumped together under the term pneumatization (or inflation). Pneumatization is by no means a simple process, even at the gross level, and certain aspects of it still defy explanation. While the literature on pneumatization is chiefly based on conditions in Homo and a few experimental animals (see DIAMANT 1940; OJALA 1950, 1957; OPHEIM 1944; SEPPÄLÄ 1946; BAST and FORESTER 1939), it is reasonable to believe that its chief features are universal.

Two types of pneumatic activity are distinguished in human otology. The first is the pneumatization of the cavum tympani, which is the membrane-lined sac derived from the first (and possibly the second) pharyngeal pouches. The second is the pneumatization of the bone tissue surrounding the cavum, which results in the various spaces (e.g., mastoid cavity, epitympanic recess, cellules, etc.) commonly found in the petrosal and other bones. The two are interactive to a certain degree, but it is important to separate them descriptively and analytically.

Very simply, pneumatization of the cavum tympani is thought to be the result of a particular form of programmed cell death, although this by itself does not explain the whole process. Early in ontogeny, the primordial cavum tympani (tubotympanic recess) expands backwards into the mesenchyme filling the area lateral to the auditory capsule, where the auditory ossicles are developing. The larger part of this mesenchyme becomes myxomatous, then undergoes atrophy. The cavum tympani expands into the atrophying areas and thus increases in volume. In attempting to explain the physiological factors involved, OJALA (1957) points out that the mesenchyme, although called 'mucoid', actually lacks a secretory function and may therefore atrophy idiopathically from 'disuse'. However, it is still necessary to explain how the cavum tympani is able to expand into areas where the tympanic mucoid tissue undergoes involution. OJALA suggests that expansion is conditioned by the action of air pressure (or the pressure of the amniotic fluid in the case of the prenatus) constantly pushing the epithelium of the cavum tympani into atrophying areas.

The end result of this form of pneumatization is that the lumen of the cavum tympani comes to occupy the whole volume of the middle ear. Nothing remains of the tympanic mucoid tissue except for a thin stratum directly beneath the epithelium of the cavum tympani.

Pneumatization of bone creates new excavations into which the expanding cavum tympani inflates. At the cellular level, this form of pneumatization is conditioned by the differential destruction and production of bone tissue, which is of course the method by which all bone remodelling occurs. It does not operate with equal intensity on all the bone surfaces facing the middle ear, but is instead highly selective in its areas of operation. Although bone cavities are formed concurrently with the inflation of the cavum tympani, it is not clear whether the latter phenomenon actually provokes bone pneumatization, or whether the two operate simultaneously but essentially independently. Observational, experimental, and pathological data have been interpreted to support both points of view; the likeliest explanation, however, is that both interaction and independent development occur, but at different times and places during ontogeny.

For example, the antrum of the human mastoid cavity is apparently formed without any relation to the expansion of the cavum tympani (OJALA 1957; RÜEDI 1937). On the other hand, the small cellules which honeycomb various parts of the temporal, and which develop much later than the antrum, are formed by the invasion of mucous membrane into marrow spaces. The marrow dedifferentiates into loose connective tissue. This is attended by the destruction of the trabeculae within the old marrow spaces and the consequent formation of small cavitations (RICHANY, ANSON and BAST 1975).

One consequence of bone pneumatization is that certain areas of older bone are completely replaced by periosteal (or woven) bone (OJALA 1957). Further, pneumatization tends to follow a particularly active course where large amounts of periosteal bone are formed. In these situations, the thin plates of periosteal bone literally migrate outwards, for rapid erosion on one surface is met with equally rapid deposition on the other. This process may be visualized as analagous to the inflation of a balloon, whereby internal volume is increased as the walls of the balloon move away from one another.

In this study, the pneumatization of the cavum tympani is not treated in any detail, and the term 'pneumatization' will therefore mean the pneumatization of bone unless otherwise specified.

Before passing on to the definition of the principal cavities, it is important to point out that pneumatization *per se* is not the only means by which the middle ear increases in volume. It also enlarges by growth along the sutures of the basicranium. Pneumatization and sutural growth cannot be sharply distinguished; the first is dominated by erosion and the second by deposition, but we have seen that pneumatization is not simply a question of osteoclastic activity. Nevertheless, it is worth preserving a distinction to the extent that this is possible, for mammals differ in the *extent* to which pneumatization occurs. Many lipotyphlans, for e[illegible]ple, have relatively small middle ears simply because pneumatization does not occur to any significant degree. In these cases, changes in volume and proportions during ontogeny are effected by slow accretionary growth at sutural interfaces combined with a limited amount of remodelling. In strepsirhines, on the other hand, both processes are important. Sutural growth markedly increases the length and width of the dorsal wall, while intense pneumatic activity swells the ventral wall.

It is peculiarly difficult to avoid a geometrical style of definition with air spaces, since they are not solid structures. Most authors rely heavily on position when defining such spaces, but this procedure sometimes conceals more than it explains. A combination of position and method of development provides somewhat more informative definitions.

The *tympanic cavity proper* may be positionally defined as the space that contains the principal organs of hearing which lie within or front upon the middle ear (auditory ossicles, fenestrae, and tympanic membrane). Other spaces may develop at specific places around its circumference through pneumatization alone or a combination of pneumatization and sutural growth. Only one such space appears to be universal in placentals; this is the epitympanic recess, which is excavated from the roof of the middle ear. It is not uncommon, however, for pneumatic activity to spread from the epitympanic recess to other areas. One such area is the lateral wall of the auditory capsule in the region of the lateral semicircular canal. If the degree of pneumatization is sufficient, a large chamber may be excavated at this position. It seems reasonable to regard this chamber as the homologue of the human antrum, although the squamosal is not always involved in other species (cf. RICHANY, ANSON and BAST 1975). More rarely, pneumatization strikes medially into the roof of the promontory itself. In lorises, excavation is so extensive that it penetrates not only the roof but also the medial side of the petrosal. The cavity so produced is distinguished here as the medial accessory cavity (of the epitympanic recess).

All of the cavities named so far are reasonably simple to identify because they are usually divided off from the tympanic cavity proper by pronounced constrictions or septa. There are other cavities, however, for which a positional definition is difficult and perhaps useless. The only one of concern here is the hypotympanic sinus. Strictly speaking, the hypotympanic sinus should lie beneath the tympanic cavity proper, but the term is often used to describe the whole volume circumjacent to the small area containing the auditory ossicles. Furthermore, in most cases the hypotympanic sinus opens so broadly into the tympanic cavity proper that it is hardly worth distinguishing the two.

Septa are not particularly significant structures, and notes on their development are chiefly aimed at a re-appraisal of SABAN's (1956-57, 1963) method for distinguishing different parts of the hypotympanic sinus. They may arise in various locations, and are usually but not always the products of pneumatic activity.

1.4.4 MUSCLES, NERVES AND ARTERIES

The sections devoted to original observations end with brief accounts of the more important soft tissues of the middle ear.

1.4.4.1 Muscles

Only two muscles are usually found within the confines of the middle ear, the tensor tympani and the stapedius. Details on their major attachments are provided in appendix II. Descriptions are confined to short notes on their form and chief relations.

Part or all of the origin of each muscle is accommodated within bony depressions (fossa for the tensor tympani and fossa for the stapedius muscle). Since these fossae are the only indications of these muscles in macerated or fossil skulls, they too receive treatment in the text.

The fossa for the tensor tympani is normally situated on the upper margin of the promontory and the adjacent epitympanic wing of the petrosal (when the latter is present). However, fibers of this muscle generally take origin from more anterior points as well, such as the sphenoid, cartilage of the tube, and the membranous covering of the piriform fenestra (WERNER 1960; HENSON 1961). Other variations in origin are also possible. Rarely, the tensor tympani is partly enclosed by bone (e.g., semicanal for tensor tympani of *Homo*).

The fossa for the stapedius muscle lies within the marked depression defined by the gyrus of the lateral semicircular canal, on the ventral surface of the pars canalicularis (fig. I-2). However, the fibers of the stapedius take origin from only a small part of this pit, and it is not correct to style the whole area as the fossa for the stapedius. The position of the fossa for the stapedius has an important bearing on the interpretation of the CTPP (see 1.4.1.3).

1.4.4.2 Nerves

In classical comparative embryology, description of nerves in the environs of the auditory region was usually limited to an account of the routes of the facial and chorda tympani. These nerves enjoyed this distinction because their relationships to other structures lent support to REICHERT's theory regarding the homologies of the auditory ossicles (GOODRICH 1930; DE BEER 1937; STARCK 1967).

However, the facial and the chorda tympani are not the only nerves which traverse the middle ear, and it occurred to me that it would be worthwhile to include notes on these others as well. Their taxonomic and morphological interest turned out to be rather low, in the sense that their routes and interconnexions do not appear to vary greatly among mammals. On the other hand, I studied only their tympanic sections, and at a rather gross level at that. A more thorough investigation might establish that greater variability exists.

The following list is an abstract of the systematic classification of the nervous system adopted by the *Nomina anatomica* (3rd ed.) and the *Nomina anatomica veterinaria* (1st ed.), slightly modified for present purposes. This list functionally associates the different parts of the nervous system which are of interest here. All entries are referred to in the text, but the underlined ones receive the bulk of descriptive treatment. Definitions and other notes may be found in appendix II, and fig. I-4 schematically illustrates major trunks and ganglia. Exceptionally detailed remarks on innervation in primates and *Tupaia* may be found in SABAN's (1963) monograph.

PERIPHERAL NERVOUS SYSTEM

- Cranial nerves
  - Trigeminal (V) nerve
    - Pterygopalatine ganglion
      - *Nerves of the pterygoid canal*
        - *Greater petrosal nerve*
        - *Deep petrosal nerve*
    - Otic ganglion
      - *Lesser petrosal nerve*
  - *Facial (VII) nerve*
    - Geniculate ganglion
    - *Greater petrosal nerve*
    - *Chorda tympani nerve*
  - Glossopharyngeal (IX) nerve
    - Distal ganglion
      - *Tympanic nerve*
        - Tympanic plexus
        - *Lesser petrosal nerve*
  - Vagus (X) nerve
    - *Auricular ramus*

AUTONOMIC NERVOUS SYSTEM

Cephalic and Cervical Part of the Autonomic System

- Pterygopalatine ganglion
- Otic ganglion
- Cranial cervical ganglion
  - Internal carotid nerve

1.4.4.3 Arteries

The tympanic branchings of the carotid system, together with associated features like the placement of arterial foramina, have become a rich source of taxonomic characters in both paleontology and neontology. Arterial patternings are known for representatives of all the families investigated here, and I cannot claim to have found much that is new. However, microscopal study of sectioned materials has permitted me to add a few details to the primary literature on these vessels.

Investigation was limited to the tympanic segments of the following members of the carotid system (not all of which occur in any one form):

- Internal carotid artery
  - Promontorial artery
    - Artery of the pterygoid canal
  - Stapedial artery
    - Ramus posterior of the stapedial artery
    - Ramus inferior of the stapedial artery
    - Ramus posterior of the stapedial artery
- Anterior carotid artery
  - Rete mirabile of the anterior carotid artery

These vessels are defined in appendix II, and fig. I-4 is a pictorial representation of their routes and connexions in an imaginary mammal.

Table 1-2

SOME IMPORTANT DERIVATIVES OF BRANCHIAL ARCHES I-III

	Ectodermal Derivatives		Entodermal Derivatives		Mesodermal Derivatives		
Arch or Pouch	Ectodermal Branchial Groove	Ectodermal Covering Of Arch	Entodermal Lining of Arch	Entodermal Pharyngeal Pouch	SKELETON	MUSCLES (and their nerves)	AORTIC ARCHES
I	External acoustic meatus Epithelium of meatus (membranous meatus) and tympanic membrane (cutaneous stratum)	Epidermis of auricle (tragus and crus helicis)	Epithelium of pharynx (part)	Lumen and epithelium of tympanic cavity and accessory spaces (part) auditory tube Epithelium of tympanic membrane (mucosal stratum)	Meckel's cartilage Malleus, incus (part) Auricular cartilage	Tensor tympani m. (tensor tympani n. V)	A. of the pterygoid canal
II	--	Epidermis of auricle (rest)	Epithelium of pharynx (part)	Lumen and epithelium of tympanic cavity and accessory spaces (part)	Reichert's cartilage Tympanohyal stylohyal, ceratohyal Stapes, malleus, incus (part)	Stapedius m. (stapedius n. VII)	Stapedial a.
III	--	--	Epithelium of pharynx (part)	--	Basihyal, thyrohyal	--	Stem of internal carotid a.

CHAPTER TWO

LEMURIFORMES

METHOD OF DESCRIPTION

2.1 VENTRAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

- 2.1.1 Fibrous Membrane of the Tympanic Cavity
- 2.1.2 Cartilage of the Auditory Tube
- 2.1.3 Tympanic Processes of the Petrosal
- 2.1.4 Ectotympanic
- 2.1.5 Relationship of the Ectotympanic and Petrosal Plate
- 2.1.6 Linea Semicircularis
- 2.1.7 'Anulus Membrane'
- 2.1.8 Other Tympanic Processes

2.2 DORSAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

- 2.2.1 Tegmen Tympani, Epitympanic Wing of the Petrosal, and Reichert's Cartilage
- 2.2.2 Epitympanic Wing of the Sphenoid
- 2.2.3 Epitympanic Wing of the Squamosal

2.3 PRINCIPAL SPACES AND SEPTA OF THE MIDDLE EAR

- 2.3.1 Principal Spaces
- 2.3.2 Principal Septa

2.4 MUSCLES, ARTERIES AND NERVES OF THE MIDDLE EAR

- 2.4.1 Ossicular Muscles
- 2.4.2 Arteries
- 2.4.3 Nerves

2.5 SUMMARY OF PRINCIPAL FINDINGS

2.1 VENTRAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

The bony ventral wall (fig. II-3) is roughly hemispherical in shape in all surviving lemurs, and is entirely formed by an outgrowth of the petrosal (the petrosal plate). Pneumatization greatly alters the form of the bulla during ontogeny. Besides causing the petrosal plate to swell out ventrally (thus forming a hypotympanic sinus of broad dimensions), pneumatic activity plays an important role in the process which leads to the unique ectotympanic-petrosal plate relationship characteristic of all modern and most fossil lemurs.

Despite occasional statements to the contrary in the literature, there is no ontogenetic evidence for an entotympanic element in the lemuriform bulla.

Muscular processes on the surface of the bulla are absent except in the region of the tubal canal, where the styliform process is situated.

2.1.1 FIBROUS MEMBRANE OF THE TYMPANIC CAVITY

In the youngest specimen of Microcebus murinus (MPIH 1964/41), the fibrous membrane is sharply defined and clearly separates the cavum tympani and the tympanic mucoid tissue from adjacent soft tissues (fig. II-4). Along the line where it leaves the ventral surface of the promontory in order to pass around the ectotympanic,

Table 2-1

LEMURIFORMES

SPECIMENS	No.	CRL[1]	HL[2]	ST[3]	PS[4]	STAIN(S)
CHEIROGALEIDAE						
Microcebus murinus						
I. Fetus	MPIH 1964/41	34.5	16.5	10	cross	Azan, Delafield
II. Fetus	MPIH 1962/57	37.0	19.0	15	cross	Azan
III. Fetus	MPIH 1964/43	41.0	21.0	10	cross	Azan, Delafield
IV. Fetus	MPIH 1964/42	41.0	21.0	10	cross	Azan, Delafield, H.& E., Heidenhain-Woelke
LEMURIDAE						
Lemur catta						
V. 10 Days Postnatal	MPIH 1964/28	—	—	12	cross	Azan
INDRIIDAE						
Propithecus sp.						
VI. Fetus	AI 210/211	—	26.0	40	cross	Azan

[1] Crown-rump length (in mm)

[2] Head length (in mm)

[3] Section thickness (in mμ)

[4] Plane of sectioning

NOTES ON SPECIMENS

With one exception (MPIH 1962/57), the specimens of M. *murinus* were collected from pregnant females trapped in Madagascar (STEPHAN 1963). *M. murinus* MPIH 1962/57 was obtained from an American supplier, but there are no details about the purchase in the MPIH catalogue. *L. catta* MPIH 1964/28 died at the Zoo Frankfurt/M.

Prof. Dr. D. STARCK (Anatomisches Institut, J.-W.-Goethe Universitate, Frankfurt/M.) kindly allowed me to study the sections and reconstruction of a *Propithecus* fetus previously described by him (STARCK 1962). It is unknown which of the two species of *Propithecus* the specimen represents.

With the obvious exception of *L. catta* MPIH 1964/28, all specimens were prenatal and appear to be in the later phases of fetal life.

Macerated skulls of adult specimens of *Lemur catta*, *Lepilemur mustelinus*, *Microcebus murinus*, and *Cheirogaleus major* from the collections of MPIH were also available for study.

it borders a low rampart of bone--the rostral tympanic process of the petrosal. The rostral tympanic process develops adjacent to, but not within, the fibrous membrane (fig. II-9). Posterior to the cavum tympani and the ectotympanic, the fibrous membrane blends into the fasciae and dense connective tissues lining the lateral wall of the auditory capsule (fig. II-16).

Conditions are much the same in MPIH 1962/57; however, the fibrous membrane appears less distinct due to the intense osteoblastic activity surrounding the trabeculae of the developing rostral tympanic process. By this stage, the fibrous membrane is so closely appressed to the periostea of the promontory and the ectotympanic that it can be separately identified only with difficulty (fig. II-10).

In the two older specimens of M. murinus (MPIH 1964/43 and MPIH 1964/42), the fibrous membrane is completely fused with the periosteum of the petrosal plate (fig. II-12), although it can still be detected as a separate membrane in the area of the ectotympanic.

In the specimen of Propithecus sp. (AI 210/211), conditions are like those in M. murinus MPIH 1964/41). The rostral tympanic process of the petrosal has only just begun development, and as in Microcebus the outgrowth forms adjacent to the fibrous membrane rather than within it. In this specimen alone the fibrous membrane has an apparent extension into the forward part of the presumptive tympanic cavity. A membrane which is dorsally continuous with the perichondrium of the cartilage of the tube closes off a small sinus with the aid of the fibrous membrane (fig. II-31).

The fibrous membrane cannot be differentiated from the periosteum of the bulla in the postnatal specimen of Lemur catta (fig. II-13).

2.1.2 CARTILAGE OF THE AUDITORY TUBE

2.1.2.1 Structure, Relations and Development

The conformation and relations of the cartilage of the tube were similar in all specimens; there were some minor differences in size and shape.

In the specimens of Microcebus, the cartilage of the tube is a free, small piece of cartilage at the anterior end of the auditory region. It has an oblique, anteromedial-posterolateral orientation and extends backwards beneath the developing alisphenoid to the anterior end of the tegmen tympani (figs. II-1,2). The cartilage folds in on itself, and it thus appears hook- or staff-shaped in cross-sections. It is not firmly fixed to any bony element in the stages represented, although the developing petrosal plate has partly surrounded it from the ventral in the oldest specimen (MPIH 1964/42; fig. II-25).

No specimen shows posterior spurs or structural subdivisions of the cartilage of the tube. In MPIH 1964/42, however, there is an isolated rod of cartilage situated close to the medial margin of the cartilage of the tube on one side (fig. II-2). Histologically, there was no difference between this cartilage and that of the auditory tube.

The cartilage of the tube appears very small relative to the grossly inflated anterior part of the bulla in Lemur catta MPIH 1964/28 (fig. II-34). The medial margin of the cartilage is thrown into numerous folds, but otherwise it is similar in essential structural features to that of the Microcebus fetuses. Since bullar development is nearly complete in this specimen, a well-marked tubal canal is present which encloses part of the cartilage of the tube.

In the specimen of Propithecus sp., the cartilage of the tube is proportionately thicker and wider than it is in Microcebus and Lemur, but it is otherwise similar in morphology (fig. II-31). The only peculiarity is the membrane which stretches between the ventral surface of the cartilage and the fibrous membrane of the tympanic cavity mentioned earlier (fig. II-31). The sinus thus enclosed is, at this time, filled with mucoid tissue, and in any event has no primary connection with the actual auditory tube.

The cartilage of the tube was not preserved in any of the macerated adult specimens available for study, but it is quite safe to conclude from the sectioned material that the cartilage does not take part in or contribute to the formation of the bony bulla.

2.1.2.2 Discussion

There is no reason to conclude that the small accessory cartilage found in Microcebus MPIH 1964/42 represents a reduced rostral entotympanic. VAN DER KLAAUW (1922) encountered such accessory cartilages in several mammals, including those with well-defined rostral entotympanics, but did not conclude that they themselves could be considered entotympanic in origin. Accessory cartilages adjacent to the cartilage of the tube are known in man (BLOOM and FAWCETT 1968:816; PROCTOR 1967:508) and are without general significance.

2.1.3 TYMPANIC PROCESSES OF THE PETROSAL

2.1.3.1 Introduction

The composition of the bulla in lemurs has occupied the attention of numerous investigators over the years (VAN KAMPEN 1905; GREGORY 1910, 1915, 1920; LE GROS CLARK 1925, 1959, 1971; VAN DER KLAAUW 1931; LAMBERTON 1941; SABAN 1956-57, 1963; VAN VALEN 1965; MCKENNA 1966; SZALAY 1969, 1972a, 1972b, 1975; CARTMILL 1975). In particular, interest has focused on the significance of its marked similarity to the tupaioid bulla. Is this similarity due to a substantial shared ancestry or to convergence? Before discussing this important question, it is necessary to supplement the available data on bullar development in lemurs so that meaningful comparisons can be made to conditions in tupaioids.

Considering the emphasis that has been placed on the mode of origin of the bulla in primate taxonomy, it is surprising that so few original investigations of conditions in young specimens have been carried out. Although it was established as early as 1844 by KOSTLIN that the lemuriform bulla arose from the petrosal (and not from the tympanic; see VAN KAMPEN 1905, for the earlier literature), the only original reports of any real value appear to be those of WINGE (1895 [1941]) and FORSYTH MAJOR (1899). VAN KAMPEN (1905) is often cited as the authority on bullar development in lemurs, but his descriptions chiefly rely on the very brief accounts of these two authors. He apparently had some young specimens for study judging from his short comments on general bullar development in prosimians (1905:677-679), but he made little use of them in his analyses. Except for a handful of parenthetical statements by later authors (e.g., CARTMILL 1975), virtually all published knowledge on bullar development in lemurs thus stems from these three sources. Contributions from comparative embryology on chondrocranial development in lemurs (HENCKEL 1927, 1928; FREI 1938; BÄHLER 1938; STARCK 1962) have generally dealt with specimens which were too young to show significant bullar development, and, in any case, have not been centrally concerned with the question of middle ear enclosure.

WINGE examined two specimens, a ?Propithecus embryo (23 mm HL) and a Lemur collaris[1] neonatus (38 mm HL). For the specimen of ?Propithecus it was noted only that the ectotympanic was ossified but the bulla was not yet formed. In the newborn Lemur collaris, WINGE found an "os bullae" which was "separated from all the surrounding bones except Pars mastoidea, from which it seems to extend as an outgrowth" (1895 [1941]:334).

FORSYTH MAJOR (1899:987-988) described bullar development in a series of single specimens from different genera:

> In the youngest stage available to me for examination, the foetus of a Chiromys[2], there is no trace of an

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[1] Lemur macaco collaris.

[2] Daubentonia.

> osseous bulla; the completely ossified annulus lies almost horizontally underneath the periotic. In a second stage (Lepidolemur[1]) ossification begins to be developed from the lower sharp margin of the periotic, which adjoins the annulus. In a third stage (Lepidolemur) this outgrowth appears increased, and has a shell-like shape, with the concavity turned outward; the annulus is gradually being uplifted by it. In a fourth stage (Lemur rubiventer) the shell-like ossification is still more increased, and begins to cover the median part of the annulus; and this state of things is still more increased in the fifth (Lepidolemur) and sixth stage (Avahis laniger[2]), with the result that first the median part, and eventually the remainder of the annulus becomes invisible when viewed from below, being shut by the periotic. In the adult...the annulus is represented by a bony ring--the size is scarcely larger than in the youngest stages-- which hangs freely in the tympanic cavity, being coalesced with the squamosum only in one part, viz. anteriorly to the stylo-mastoid foramen. Ontogeny thus teaches us that the annulus of the adult is not a secondarily detached part of the bulla.

Both investigations, as a result of their lack of detail, invite questions. The most significant query, in my view, concerns the site of origin of the petrosal bulla. Not only is FORSYTH MAJOR's "lower sharp margin of the periotic, which adjoins the annulus" uninformative, but it is also not in accordance with WINGE's claim that the 'mastoid' gives rise to the bulla. VAN KAMPEN (1905:656) noted this discrepancy, but did not attempt to resolve it. In a later passage, however (1905:677), he appears to favor FORSYTH MAJOR's interpretation. VAN VALEN (1965) suspected that there should be a mastoid component in the lemuriform bulla, although he lacked the necessary young specimens in which its presence might be demonstrated.

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[1] Lepilemur.

[2] Avahi laniger

This study establishes, in detail, that the lemuriform bulla is petrosal in origin and that there is no entotympanic (a point which the early studies did not in fact settle). Further, it establishes that both WINGE and FORSYTH MAJOR were correct if it can be assumed that the latter author meant the promontory by "lower sharp margin of the periotic", for the bulla (or petrosal plate) in lemurs is formed from both a promontorial component (rostral tympanic process of the petrosal) and a 'mastoid' component (caudal tympanic process of the petrosal). The two components lose their separate identities early in bullar ontogeny and thereafter comprise a single unit, the petrosal plate. However, certain features of development permit their anatomical separation until a relatively late stage of bullar growth. Accordingly, in the following descriptions, the parts of the petrosal plate will be separately distinguished where useful or convenient.

2.1.3.2 Structure, Relations and Development of the Petrosal Plate

(1) Conditions in Microcebus murinus Specimens

The anterior of the two outgrowths, the rostral tympanic process of the petrosal (hereafter, RTPP), initially arises from the ventral surface of the promontory. The posterior one, the caudal tympanic process of the petrosal (hereafter, CTPP), arises partly from the most posterior part of the promontory and partly from the anteroventral surface of the pars canalicularis. The basic relations of the processes to the rest of the auditory capsule are depicted in the reconstruction of MPIH 1962/57 (fig. II-1).

The RTPP is the low ridge of bone extending in an even curve from the anterior pole of the promontory to the level of the medial wall of the apertura fossulae fenestrae cochleae (hereafter, MWF). The CTPP is the more irregular, cartilaginous rampart which extends around the posterior part of the presumptive tympanic cavity. The MWF marks the anatomical termination of the promontory, and its ventrolateral margin is the only part of the promontory which contributes to the CTPP. The MWF is also the meeting place of the RTPP and CTPP; as can be seen from the reconstruction, the two outgrowths are already in contact at this stage of development. Together, they form a single process of complicated shape (the petrosal plate), although their point of meeting can be distinguished in this and other fetuses by certain structural features (see following descriptions).

The RTPP evidently arises somewhat later than the CTPP, for it is a periosteal outgrowth and does not begin development until the ventral surface of the promontory is ossified. The CTPP arises in cartilage, probably soon after the initial chondrification of the posterior part of the auditory capsule. Perhaps the fact that the CTPP is initially larger than the RTPP led WINGE to describe the whole petrosal plate as a mastoidal outgrowth. RAMASWAMI (1957) makes a similar mistake in regard to bullar development in *Loris tardigradus* (see 3.1.3).

Microcebus murinus MPIH 1964/41

In this youngest representative of Microcebus, the RTPP is represented only by a discontinuous line of delicate trabeculae. At this stage the RTPP projects only a slight distance from the ventral floor of the promontory, and would easily be missed if older stages were not available for comparison. The trabeculae are disposed as in the reconstruction of MPIH 1962/57 (fig. II-1), except that they terminate just anterior to rather than on the MWF. The trabeculae are contained within the periosteum of the promontory, which appears thickened and diffuse in the area of the RTPP (fig. II-9). Large numbers of preosteoblasts and osteoblasts densely coat these trabeculae.

The disposition of the RTPP can be correlated with two other features. First, the RTPP is situated above and slightly medial to the ectotympanic where this bone curves beneath the promontory; there is thus a close correspondence between the arc described by the ectotympanic and that described by the RTPP. Secondly, the fibrous membrane of the tympanic cavity leaves the promontory to attach to the ectotympanic along the same arc; in effect, the fibrous membrane bounds the medial side of the thickening of the promontorial periosteum containing the RTPP. The significance of this is that the RTPP is situated from the first along the medial wall of the primordial tympanic cavity (as defined by the fibrous membrane), despite the fact that this process initially arises from the middle of the ventral surface of the promontory.

The CTPP arises from several structures or morphological areas which have been terminologically differentiated by comparative embryologists. It is worthwhile distinguishing these areas and structures to the extent that they facilitate description and comparison of specimens; however, we shall be concerned with them only insofar as they relate to the production of the CTPP.

Medial, posterior and lateral subdivisions of the CTPP may be discriminated (see 1.4.1.3). The medial section is mostly formed by the MWF, the 'processus recessus' of comparative embryology. At the stage of development represented by MPIH 1964/41, the MWF is only slightly ossified (figs. II-16, II-17); it extends from the cochlear floor to the anteroventral surface of pars canalicularis, thus producing a floor and medial and lateral apertures for the recessus scalae tympanic (DE BEER 1937; FRICK 1952, 1954). The MWF flares out laterally where it communicates with the pars canalicularis, so forming a distinct shelf which may be identified as the medial section of the CTPP. This shelf continues posteriorly beyond the morphological end of the MWF, and ends at the site of the joint foramen for the tympanic nerve and the auricular ramus of the vagus (figs. II-16, II-17).

The posterior portion of the CTPP consists of a low, cartilaginous elevation running from the joint foramen mentioned above to the site of origin of the stapedius muscle. It is disposed mediolaterally on the floor of the pars canalicularis (fig. II-17). It is not as broad as the medial portion of the CTPP and loses height near the origin of the stapedius.

The lateral section of the CTPP is very poorly defined in fetuses of _Microcebus_ (although it is large in _Propithecus_ sp. AI 210/211). It is no more than a slight protrusion of the ventrolateral face of the auditory capsule beneath the prominence of the lateral semicircular canal (figs. II-16, II-17). The lateral portion of the CTPP is properly the posterior continuation of the crista parotica (see 1.4.1.3), and it extends from the origin of the stapedius muscle to the root of Reichert's cartilage (where it is crossed by the facial nerve).

Considered together, the three morphological parts of the CTPP in _Microcebus_ constitute an incomplete hood of cartilage which partially covers the most posterior part of the presumptive tympanic cavity. Ossification is found only in the medial portion at this stage.

The RTPP and CTPP can be validly regarded as separate structures to the extent that they arise at different times in different ways from different major divisions of the auditory capsule (pars cochlearis and pars canalicularis). In MPIH 1964/41, the two processes are not yet in contact because the trabeculae of the PTPR have not reached the ventral surface of the MWF.

Microcebus _murinus_ MPIH 1962/57

This specimen shows some advance over conditions in MPIH 1964/41. The RTPP has increased in height and in length. The trabeculae constituting it now form a continuous ridge and the local thickening of the periosteum of the promontory is more pronounced. The ectotympanic and the RTPP lie in closer proximity; the RTPP is now situated directly above the medial margin of the ectotympanic rather than slightly dorsomedial to it as in MPIH 1964/41 (fig. II-10). This is significant, for the intimate relationship thereby produced is a characteristic feature of development which continues until a relatively late stage in the ontogeny of the bulla.

In the reconstruction (fig. II-1), it can be seen that the trabeculae of the RTPP extend to the limit of the anterior pole. Whether they extend beyond this, i.e., onto the front of the anterior pole, could not be determined because of the angle at which the specimen was cut. Later stages, however, demonstrate that the RTPP eventually extends from the rostral and superior parts of the anterior pole as well.

Increase in the length of the posterior part of the RTPP is more easily identified. Instead of ending at the position of the medial wall of the apertura fossulae fenestrae cochleae as in MPIH 1964/41, the trabeculae of the PTPR now extend from the ventral surface of the MWF itself. The trabeculae of the RTPP are oriented at nearly a right angle relative to the plane of the medial wall of the apertura, and therefore can be clearly distinguished from the latter (fig. II-20). In this specimen, the RTPP terminates by swinging laterally across the ventral face of the MWF; in serial sections, it appears to end suddenly in a cave-like formation. This is another feature which allows the continued differentiation of the RTPP and CTPP after the two form a single structural unit, the petrosal plate.

The CTPP is slightly more developed than in MPIH 1964/41, although it does not cover much more of the posterior part of the presumptive tympanic cavity than in the previous fetus. The CTPP is slightly more ossified, but most of the posterior and lateral sections remain cartilaginous (fig. II-21).

Microcebus murinus MPIH 1964/43

The petrosal plate has grown a significant amount compared to conditions in MPIH 1962/57.

The greatest elaboration of the petrosal plate has occurred in the area of the anterior pole of the promontory. Some features characteristic of the adult can be identified in their early stages of development. VAN KAMPEN (1905:678) noted that the bulla defines part of the roof of the tympanic cavity in lemurs, separating it from the cranial cavity (see 2.2.1). In this specimen there is a broad, thin lamina of bone which projects freely from the anterior face of the anterior pole. Conditions in this and later fetuses suggest that this anterior projection gives rise to the massively inflated, cavernous anterior portion of the bulla. The anterior projection displays a complex structure even at this relatively early stage of development. In cross-sections immediately in front of the promontory, the anterior projection appears as a thin lamina deeply excavated on its lateral surface (fig. II-22). Its participation in the roof of the tympanic cavity is already evident. Its lower half represents a continuation of the arc described by the rest of the petrosal plate, and like the rest of the part of the plate derived from the RTPP, its inferior margin is associated closely with the ectotympanic. Its upper half, besides contributing to the roof of the tympanic cavity, gives origin to a pointed spur of bone which diverges anteromedially from the rest of the anterior projection. This spur, through its continued development, eventually forms the anteromedial process of the bulla found in the adult. The reconstruction of MPIH 1964/42 depicts the anteromedial process and the anterior projection in a slightly older embryo (fig. II-2).

The portion of the petrosal plate derived from the RTPP descends in height from anterior to posterior. As in MPIH 1962/57, there is a well-marked cave-like structure on the ventral surface of the MWF (fig. II-23, II-24). Except for its more pronounced cavitation, it corresponds in all essential details to the similar feature in the previous embryo. Accordingly, it would appear permissible to suggest that the zone of continuity between the primordial RTPP and CTPP is still discernible.

Osteoclasts are detectable along the entire lateral face of this part of the petrosal plate, while osteoblasts densely coat its medial and ventral faces. One can now visualize the basic process involved in bullar inflation: osteoblastic deposition on the medial face combined with simultaneous osteoclastic erosion on the lateral face.

The bone of the part of the petrosal plate derived from the RTPP displays a structural gradation which may be significant for an understanding of certain developments in MPIH 1964/42. The superior moiety adjacent to the promontory shows typical young fibrous or woven bone; the bone tissue is quite cellular, the osteocytes are situated in large lacunae, and the intercellular matrix stains rather lightly. The inferior moiety, directly above the ectotympanic, grades into a tissue in which the lacunae are enormous and the intercellular matrix is thin and very poorly stained (fig. II-11).

A final important development is the ventral enlargement of the entire rim of the petrosal plate where it overlies the ectotympanic (fig. II-11). This feature is also seen, in even more pronounced form, in MPIH 1964/42.

The section of the petrosal plate derived from the CTPP has not developed at the same rate as the section derived from the RTPP. It is now bony throughout its medial and posterior portions as a consequence of the further ossification of the medial margin of the apertura fossulae and the adjacent parts of the pars canalicularis. The lateral portion is partly bony as a result of the ossification of the auditory capsule in the region of the lateral semicircular canal. The part immediately adjacent to the base of Reichert's cartilage remains cartilaginous.

Microcebus murinus MPIH 1964/42

Although MPIH 1964/42 has the same measurements as MPIH 1964/43, the auditory region is more developed and the petrosal plate is larger.

As in MPIH 1964/43, the anterior projection arising from the anterior pole of the promontory has grown at a faster rate than the remainder of the petrosal plate. The medial section, which is destined to become the anteromedial process of the bulla, is somewhat longer and attains the posterior wall of the foramen for the anterior carotid. The base of the presumptive anteromedial process where it joins the rest of the anterior projection is slightly cavitated (fig. II-12); it is apparently in the first stages of inflation. The remainder of the anterior projection conforms to the arc of the promontorial section of the petrosal plate, as in the preceding specimen. The superior part of the anterior projection helps to complete the roof of the tympanic cavity (fig. II-12). A new feature is a small lip of bone which extends from the anterior projection beneath the medial part of the cartilage of the tube, thus forming an incomplete tubal canal (fig. II-25).

The section of the petrosal plate extending from the ventral surface of the promontory is slightly longer than in MPIH 1964/43, but it shows no significant degree of medial displacement. Obviously, there has been considerable growth in length without a marked degree of inflation in the available ontogenetic series.

An interesting and unusual feature of the petrosal plate in this specimen is the histological nature of the ventral enlargement: the cells and intercellular matrix of the enlargement are reminiscent of hypertrophied cartilage rather than young bone (fig. II-26, II-27). This cartilage-like tissue occupies the entire ventral surface of the petrosal plate where the plate is in direct association with the ectotympanic but not elsewhere. Thus it is absent from most of the portion of the plate derived from the CTPP (which has not yet attained the posterior crus of the ectotympanic) and from all but the ventral part of the anterior projection.

Lack of sectioned specimens older than MPIH 1964/42 prevents a secure identification of this tissue; however, there appears to be no good reason to consider it as other than secondary cartilage (definitive secondary cartilage of MOSS 1958), a tissue of common occurrence in bones and processes of dermal origin (e.g., squamosal, palatine).

With Azan, the ventral enlargement has the following appearance. Definite bone, stained reddish-blue, composes the superior part of the petrosal plate adjacent to the promontory. A thin splint of tissue similar in color extends down the medial face of the ventral enlargement. The cartilage-like tissue occupies the medial section of the lower third of the petrosal plate. The splint, apparently bone, grades into this tissue without any interruption or clear demarcation.

There is also a gradation in the histological features of the ventral enlargement. Its topmost part is composed of cells which are rather shrunken but nonetheless larger than those of the splint (fig. II-12). The majority of the cells are rather darkly stained and are enclosed in spacious, well-defined lacunae. Darkly-stained giant cells (chondroclasts or osteoclasts) are found in this uppermost area, as are a few empty lacunae. The intercellular matrix is blue to reddish-blue and sparse, giving this part of the ventral enlargement a honeycombed appearance.

This zone grades inferiorly into one in which the cells are pale-staining and not shrunken. In this area the walls of the lacunae are light blue and somewhat thicker. This zone finally grades into one in which the matrix is virtually colorless and densely cellular.

That the appearance of the ventral enlargement is not due to an artifact of the Azan stain is demonstrated by similar differences between definite bone and the cartilage-like tissue in sections stained with hematoxylin and eosin, Heidenhain-Woelke, and Delafield. Although the latter two are not routinely used as connective-tissue stains, there is a marked difference in the degree to which they stain bone and cartilage. Bone cells, cartilage cells and bone matrix stain black, while cartilage matrix either does not pick up stain at all or colors a very pale brown. Precisely these differences were found in the petrosal plate, the matrix of the ventral enlargement being virtually colorless (fig. II-27).

It was noted in the discussion of the petrosal plate of MPIH 1964/43 that the matrix of the ventral edge of the petrosal plate stained very poorly with Azan and the lacunae in this area were extremely large. However, there is nothing which suggests the secondary cartilage of MPIH 1964/42.

The section of the petrosal plate derived from the CTPP has grown substantially, as can be seen in the reconstruction (fig. II-2). The posterior part of the tympanic cavity has been largely closed off, and the foramen stylomastoideum (definitivum) is virtually complete due to the growth of the plate around the base of Reichert's cartilage. The free anterior margin of this part of the plate, which is deeply incised where the internal carotid enters the tympanic cavity, now almost reaches the posterior crus of the ectotympanic.

The posterior part of the petrosal plate is now bony throughout except for a small area adjacent to Reichert's cartilage.

(2) Conditions in Propithecus sp. AI 210/211

The RTPP of this specimen resembles that of MPIH 1964/41 in that only discontinuous trabeculae are to be found on the ventral floor of the promontory adjacent to the fibrous membrane of the tympanic cavity.

The CTPP is cartilaginous and moderately larger than that of MPIH 1964/41 (see STARCK 1962:171, fig. 3, "Proc. mastoideus"). In general structure the CTPP is quite similar to that of Microcebus and does not require detailed description. The lateral section of the CTPP is well-developed (fig. II-32), and the origin of the stapedial is already covered.

(3) Conditions in Lemur catta MPIH 1964/28

The method of development of the petrosal plate cannot be determined because of the age of this specimen, although it is probable that Lemur possesses both a RTPP and a CTPP.

The petrosal plate of the young juvenile differs in minor details from that of the adult, and most of these are connected with the degree of bullar inflation. Anteriorly (fig. II-34), the diverticula of the anterior wall of the bulla (see 2.3.1) are present and there is a well-developed tubal canal. The bulla contributes to the superior wall of the tympanic cavity medial to the tegmen tympani, as in Microcebus (fig. II-8).

The petrosal plate grows and inflates at a greater rate in its anterior part than in its posterior, as in Microcebus. In the young juvenile, the petrosal plate is still situated on the ventral surface of the promontory, thus exposing a portion of the medial wall of the latter along the petrosal-basioccipital suture.

There is a deep diverticulum of the tympanic cavity which extends between the medioventral side of the floor of the promontory and the petrosal plate; it is bordered laterally by the posterior septum (fig. II-35, II-36). This diverticulum becomes larger as a result of the inflation of the posterior part of the petrosal plate later in ontogeny, and is visible in the adult as the cavern beneath the bony carotid canal.

The fact that the bulla is still undergoing inflation is indicated by the lack of lamellar bone or Haversian canals in most areas. The floor of the hypotympanic sinus appears to be a particularly active area of external deposition and internal erosion (fig. II-8).

There is no sign of secondary cartilage anywhere in the petrosal plate, including the area of the external auditory meatus (where it might be expected on the basis of conditions in MPIH 1964/42).

2.1.3.3 Discussion: Significance of Secondary Cartilage in the Petrosal Plate

The occurrence of secondary cartilage in the petrosal plate of MPIH 1964/42 requires explanation, as it may be thought that this tissue constitutes evidence of an entotympanic in modern lemurs. A full consideration of the entotympanic problem will be left until the entotympanics of Tupaia and Elephantulus have been described and compared with those of other mammals, for the problem as it relates to primates has both historical and phylogenetic aspects. If it were not for the earlier active espousal of tupaioid-primate affinities by several influential workers, it is quite doubtful that the debate over the existence of the entotympanic in ancestral and modern lemurs would have arisen.

At least three major positions have been taken on the entotympanic problem with regard to lemurs:

(1) The bulla of modern lemurs is formed by the entotympanic (e.g., GREGORY 1910:322; LE GROS CLARK 1926:1295).

(2) The entotympanic was present in the ancestral insectivore-primate stock, but was lost in the line leading to primates and functionally replaced by the petrosal plate (e.g., MCDOWELL 1958:205; MARTIN 1968b:399).

(3) The entotympanic fused with the petrosal earlier and earlier in ontogeny during lemuroid phylogeny, until it finally lost its developmental independence altogether. It now appears as a direct outgrowth of the petrosal (e.g., VAN KAMPEN 1905:362-366; SPATZ 1966:47).

There are several other viewpoints which are based largely on the converse proposition that the entotympanic of tree shrews is a detached petrosal plate. These will be discussed later.

Of the three views listed above, the second is potentially demonstrable by new fossil evidence. At present, however, it must be considered as an unsupported speculation (cf. SZALAY 1972b:7, n.1). The other two views, however, relate to the province of developmental anatomy and to methods of arriving at homologies by reference to ontogenetic development, and these may be reviewed here.

On what grounds are bones, as individual units, homologized? Relative position, articulations, and relationships to soft tissues are obviously of prime importance. Another consideration is the criterion of independence. If a bone has the same set of relations in two animals, and at the same time is recognizably separate from all other bones during some part of ontogeny, the demonstration of homology would appear to be relatively simple. In practice, it often is; but as DE BEER (1937:502-511) points out in his discussion of morphological units, individual ossification centers as such are not always equivalent to phylogenetically independent bones.

It is far more difficult, in every way, to assess cases where phylogenetically separate units are considered to have fused so intimately that their independence cannot be established at any stage of ontogeny. This is, however, the footing upon which the third view is advocated. VAN KAMPEN's (1905:366 [trans.]) view, which concurs with SPATZ' (1966), is that the lemuriform bulla

> ...appears to be ossified from the petrosal, although in its definitive form it displays the greatest agreement with the entotympanic of Tupaja [sic] (cartilage has not been demonstrated in either case). The suppression of the entotympanic by the petrosal could have occurred

> gradually. However, transitions in which the bulla is composed partly of the entotympanic and partly of the petrosal are not known. Provisionally, it seems to me that these conditions can best be explained through *fusion primordiale*.

The concept of *fusion primordiale* is descriptive of the situation where, in place of two phylogenetically separate bones, there is only a single rudiment even in earliest ontogeny (DE BEER 1937:505). *Fusion secondaire* refers to cases in which fusion is demonstrable during ontogeny (e.g., human frontal).

The presently-known fossil evidence, all of which is adult, cannot be used to support the notion that the entotympanic has undergone *fusion primordiale* in the ancestral line of lemurs. However, it may be thought that the strip of secondary cartilage found in MPIH 1964/42 is exactly what is predicted by this concept. There cannot be much doubt that this secondary cartilage is produced by the petrosal plate, for no separate cartilaginous rudiment was found in MPIH 1964/43 (which is very close in age to MPIH 1964/42). Under one interpretation, the secondary cartilage would represent the nearly, but not completely, suppressed rudiment of the entotympanic which now forms from the petrosal plate because of *fusion primordiale*.

There are cases in which secondary cartilage has been regarded as the remnant of a phylogenetically independent bone. The best-known example is DE BEER's (1929) argument that the pterygoid of ditrematous (eutherian) mammals is a compound bone. The ditreme pterygoid almost always displays, at some ontogenetic stage, two morphological areas. The one is composed of dermal bone and is attached to the other, which is composed of secondary cartilage. Through comparisons among a variety of animals, DE BEER came to the conclusion that the dermal part is the basitemporal or detached lateral wing of the parasphenoid, while the secondary cartilage to which it is attached is homologous with the reptilian pterygoid.

Yet in the overwhelming majority of ditremes in which this point has been carefully studied, the cartilaginous and dermal parts of the pterygoid are never separate (although there is some variation in which segment appears first; ELOFF 1950). Thus DE BEER's interpretation is another appeal to fusion primordiale. Yet, as he himself notes (1937:505), the concept of fusion primordiale is "a dangerous precedent to go on, for there would be no check to speculative assumptions of fusion in order to explain all difficulties". Similarly, GAUPP (1895:83) rejected fusion primordiale as a completely valueless concept because of the difficulty in proving it has occurred in any given case.

Recognition of areas of secondary cartilage formation as the rudiments of phylogenetically independent bones can only lead to confusion. Secondary cartilage formation is also common, embryonically, in the postglenoid area of the squamosal, the medial margins of the palatines, and the dentary; it would be absurd to regard these as remnants of suppressed bones. Further, the term "secondary cartilage" has been used to cover an extraordinary variety of tissues which appear under very different circumstances and at different points in development. No review of the voluminous literature on the types of secondary cartilage can be undertaken here. Nonetheless, it should be noted that modern studies support the idea that, at least in some instances (e.g., the dentary), its main function is that of a growth cartilage (WEINMANN and SICHER 1955; RICHANY, BAST and ANSON 1956; YUODELIS 1966). Mechanical stress may also play a role in the appearance of secondary cartilage, at least in birds (MURRAY 1957; HALL 1968).

As a final note, it is worth pointing out that the cells which form secondary cartilage in the mandible are capable of forming either bone or cartilage. When these cells rapidly proliferate under conditions of lowered blood supply, they differentiate into cartilage cells; when the blood supply is adequate, they become bone cells (HALL 1968: 812). Economy of hypotheses leads one to the conclusion that embryonic secondary cartilage, whatever its function or functions, is an ontogenetic adaptation which provides no concrete evidence of supposed instances of fusion primordiale.

In summary, the secondary cartilage found in the petrosal plate of Microcebus murinus does not constitute unequivocal evidence for a suppressed entotympanic which has become part of the petrosal through fusion primordiale. The reason for its appearance at this site is not clear; the petrosal plate grows rapidly in Lorisiformes as well (see 3.1.3), yet I found no definite sign of secondary cartilage formation in the specimens available to me. WÜNSCH (unpubl. obs. cited in STARCK 1975) has recently confirmed VAN KAMPEN's (1905:674) statement that cartilage occurs in fetal Tarsius, but it is not clear in either reference whether this material is truly secondary cartilage or where it occurs on the petrosal plate.

Accordingly, the statements of GREGORY (1910), LE GROS CLARK (1926) and others concerning the presence of an entotympanic in modern lemurs cannot be supported on any grounds. The view of VAN KAMPEN (1905) and SPATZ (1966) cannot be completely rejected because the ontogeny of the bulla in ancient primates is unknown. On the other hand, I conclude that there is nothing in the ontogeny of the petrosal plate in modern lemurs which makes it particularly likely. The secondary cartilage occurring in fetal *Microcebus* can reasonably be regarded as an ontogenetic adaptation having nothing to do with an entotympanic, even if the role of this adaptation is not yet clear. Present fossil evidence does not directly point to either the loss or the suppression of the entotympanic in the primate line, and until such evidence is forthcoming neither the second nor the third views mentioned at the start have any special claims to plausibility.

2.1.4 ECTOTYMPANIC

2.1.4.1 Structure, Relations and Development

The ectotympanic retains a 'ring'-like appearance throughout life in lemurs, as numerous authors have mentioned (see VAN DER KLAAUW 1931 and SABAN 1963 for detailed descriptions of adult conditions). However, it is important to remember that the ectotympanic grows in diameter during ontogeny, even though its proportions remain those of the embryo.

The ectotympanic displays little variety in the available fetal stages of *Microcebus murinus*, and reference will chiefly be made to the reconstructions of MPIH 1964/42 and MPIH 1962/57.

The bone describes the better part of a circle which opens superiorly at the tympanic notch. The apex of the anterior crus is broadened and irregular in shape (figs. II-1, II-2), and, in the stages represented, is only loosely joined by connective tissue to the lateral margin of the tegmen tympani and the ventral edge of the squamosal. The superior aspect of the anterior crus bears a shallow trough, the sulcus malleolaris, which is traversed by the gonial, chorda tympani and Meckel's cartilage (latter degenerate in MPIH 1964/43 and MPIH 1964/42). The long posterior crus narrows into a spit which inserts between the auditory capsule and the base of Reichert's cartilage. The chorda tympani lacks a bony canaliculus in these fetuses and passes directly through the tympanosquamosal suture into the middle ear.

The tympanic sulcus deeply scores the inner circumference of the ectotympanic distal to the apices of the crura. It is present in all specimens, but is relatively deeper in the older ones as a result of osteoclastic erosion within the sulcus itself (figs. II-9 to II-13).

The ectotympanic is highly cellular at first, and osteocytes are randomly arranged with few processes. The matrix is relatively sparse and its contained fibers are coarse and irregularly arranged. As development progresses, the bone becomes relatively less cellular, but the random distribution of osteocytes is a persistent feature (fig. II-26). Correlated with the histological appearance of the ectotympanic is the complete absence of marrow spaces, endosteal tissue, and, surprisingly, a lack of detectable lamellization or resting lines--even though the ectotympanic must grow circumferentially in order to attain adult size. It may be mentioned here that the contrast between the organization of the bone of the ectotympanic and the highly-lamellated bone of the petrosal plate permits identification of the original ectotympanic component in the composite bullae of adult Tarsius and Galago (fig. III-24).

The lack of circumferential lamellization in fetal stages may be attributed to the fact that the ectotympanic grows as immature or woven bone; the random orientation of fibers and osteocytes may prevent the production of a laminar structure (WEINMANN and SICHER 1955). However, instead of eventually becoming mature bone, the bone of the ectotympanic assumes an 'intermediate' form which apparently persists into the adult period. WEINMANN and SICHER (1955: 42-44) describe the general features of intermediate bone in the following terms:

> In many instances a type of bone tissue can be observed that is intermediary between immature and mature lamellated bone. This type of bone is characterized by a fairly regular arrangement of typically shaped osteocytes. The number of bone cells compared to that of immature bone is also greatly reduced. The fibrils of this intermediary type thin but are still irregularly arranged. Especially the alternating direction of the fibrils in adjacent layers of bone, and therefore a clear lamellation, is still lacking.

Such intermediate bone composes the ectotympanic of L. catta MPIH 1964/28, and the ectotympanic has almost attained adult size in this specimen. For this reason I suspect that the ectotympanic of the adult would also consist of intermediate rather than mature lamellated bone.[1]

Although the cambial layer of the periosteum appears very active around the entire bone in the specimens of _Microcebus_ (figs. II-9 to II-12), there is a definite selectivity in the pattern of growth. The maximum superior-inferior width of the ectotympanic through the umbo of the tympanic membrane is 2.7 mm in MPIH 1964/41, 3.2 mm in MPIH 1964/42, and over 4 mm in the adult. The thickness of the body, however, is virtually identical (ca. 0.3 mm) in both fetal and adult specimens. That is, the ectotympanic grows significantly in width, without noticeably increasing in thickness, from the late fetus to the mature stage.

The structure and relations of the ectotympanic in the specimens of _Propithecus_ sp. and _Lemur_ _catta_ are little different from those encountered in _Microcebus_ _murinus_. The posterior crus in _L_. _catta_ MPIH 1964/28 is not yet fused with either the squamosal or the posterior metal margin of the petrosal bulla, although sutural tissues exist in this area.

In contrast to conditions in the fetal specimens of _Propithecus_ and _Microcebus_, the superior surface of the apex of the anterior crus is closely applied to the surfaces involved in the petrosquamous suture in the ten-day old Lemur catta (fig. II-8). The ectotympanic never fuses with the squamosal or petrosal at this site, but the position of the anterior crus allows one to deduce the approximate location of the (obliterated) petrosquamous suture in the adult (fig. II-3).

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[1] Lack of significant remodelling in the area of the attachment of the tympanic membrane to the ectotympanic was found by HOYTE (1961) in a series of alizarin preparations of postnatal rabbits.

Growth of the ectotympanic is virtually complete in Lemur catta by the time of birth or shortly thereafter. The maximum width through the umbo in MPIH 1964/28 is 5.5 mm, compared to an adult value of approximately 6 mm; thickness measurements are 0.58 and 0.6 mm respectively. Near-completion of growth is also indicated by the quiescent appearance of the periosteum (fig. II-13).

2.1.4.2 Inclination of the Ectotympanic

The ectotympanic undergoes relative displacement outwards as a result of the rotation of the auditory capsule, growth of the roof of the tympanic cavity, and the development of the petrosal plate. For present purposes, the processes involved in ectotympanic rotation may be reduced to two components (see below) without much loss in accuracy. The ectotympanic may be regarded as a moveable link between two hinges; these hinges comprise the soft tissues which bind the bone to the petrosal plate ventrally and the lateral part of the roof of the tympanic cavity dorsally. It can easily be seen that the relative positions of these hinges, and therefore the link between them, must alter during ontogeny. The petrosal plate, as it elongates, tends to drive the ventral part of the ectotympanic downwards; growth at the petrosquamous suture, which increases the width of the roof of the tympanic cavity, causes the anterior crus of the ectotympanic to suffer relative displacement outwards. Note that these two components of displacement operate at cross-purposes. Movement at the ventral hinge results in an increase in the angle of inclination (away from the horizontal), while movement at the dorsal hinge decreases it (towards the horizontal).

The limited number of sectioned specimens prevents closer analysis of the actual style of ectotympanic rotation in lemurs. The Microcebus series (table 2-2) suggests that the angle of inclination first decreases, then increases, during fetal life. This may represent no more than individual variation, and a larger sample might establish that the angle increases steadily during ontogeny. Alternatively, recorded values may indicate that growth at the petrosquamous suture (no doubt aided by the rotation of the auditory capsule) is the dominant influence on the positioning of the ectotympanic at first, but that it is later outstripped by the rapidly-growing petrosal plate moving the ectotympanic ventrolaterally. This latter interpretation is not unlikely; changes in the direction of ectotympanic rotation are known in other mammals (especially Homo; see FORSTER 1925).

Table 2-3 lists inclination values for the adult stages of several genera. Note, in the case of Microcebus, that only about two-thirds of the final inclination value is attained prior to birth (36.5° in the late fetus, 60° in the adult). This obviously indicates that the phenomenon of ectotympanic rotation is not entirely limited to the prenatal period. It also establishes, by inference, that the ventral hinge is not lost once the petrosal plate surrounds the ectotympanic; if it were in fact lost, the inclination of the

Table 2-2

INCLINATION OF THE ECTOTYMPANIC
IN YOUNG LEMURIFORMES

Specimen No.	Angle of Inclination L	Angle of Inclination R	Average Inclination
Microcebus murinus			
MPIH 1964/41	38°	36°	37.0°
MPIH 1962/57	30°	30°	30.0°
MPIH 1964/43	28°	27°	27.5°
MPIH 1964/42	36°	37°	36.5°
Propithecus sp.			
AI 210/211	31°	32°	31.5°
Lemur catta			
MPIH 1964/28	59°	58°	58.5°

The inclination (in this case) is the angle between the plane of the ectotympanic and the (horizontal) plane of the basicranium. Values for the inclination of the left (L) and right (R) ectotympanics differ in some cases because of individual variation and distortion of sections during histological preparation.

Table 2-3

INCLINATION OF THE ECTOTYMPANIC IN ADULT LEMURIFORMES

Genus	Angle of Inclination	Source
Lemur	47 50 - 60 50	FORSTER (1925) SABAN (1956-57) SABAN (1963)
Hapalemur	70	SABAN (1963)
Lepilemur	60	SABAN (1963)
Avahi	80	SABAN (1963)
Propithecus	72	SABAN (1963)
Indri	60	SABAN (1963)
Cheirogaleus	50	SABAN (1963)
Phaner	60	SABAN (1963)
Microcebus	60	SABAN (1963)
Daubentonia	30	SABAN (1963)

SABAN (1963) measures the angle between the sagittal plane and the ectotympanic as the inclination. The sagittal plane is very difficult to find in sectioned material because of the inevitable shrinkage of the brain and disruption of the thin bones of the vault during processing. In the interests of uniformity, I have listed the complements of SABAN's (1963) original values.

ectotympanic could not reach a value of 60°. The explanation for continued lateral movement lies with the fact that the ectotympanic remains firmly attached to the internal aspect of the bullar wall by means of connective tissue. Accordingly, lateral growth and pneumatization of the petrosal plate in the postnatal period would have the effect of further displacing the body of the ectotympanic lateralwards.

2.1.5 RELATIONSHIP OF THE ECTOTYMPANIC AND PETROSAL PLATE

2.1.5.1 Introduction

Two distinct forms of the ectotympanic-petrosal plate relationship (or EPPR) are found in modern primates. In lemurs alone, the anular ectotympanic is almost entirely concealed by the petrosal plate (aphaneric condition).[1] In adult lemurs, the posterior crus of the ectotympanic is fused with the posterosuperior margin of the petrosal plate and the inferiormost edge of the squamosal. The anterior crus is closely appressed, but not fused, to the roof of the tympanic cavity. The ventral portion of the ectotympanic is said to be 'free'; it juts into the middle ear and is joined internally to the lateral wall of the petrosal plate by soft tissue.

This condition contrasts sharply with that found in all other contemporary primates (including lorises), in which the ectotympanic is more or less completely fused to the lateral aspect of the petrosal plate and adjacent parts of the squamosal (phaneric condition).

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[1] For notes regarding terminology, see 1.4.1.3 ("Ectotympanic").

Many authors have commented on the peculiar EPPR of lemurs; a number have counted it as another special resemblance between the latter and tree shrews (in which the ectotympanic is also 'free'; see 4.1.6).

Virtually nothing is known about the ontogeny of the EPPR. For example, WINGE (1895 [1941:334]) noted that in a neonatal specimen of _Lemur collaris_[1] the

> ...external margin of this "_Os bullae_" [i.e., petrosal plate] closely surrounds _Annulus_ and assists in carrying the external cartilaginous and membranous meatus. In an adult _Lemur collaris_, "_Os bullae_" extends as in other Madagascan lemurs, around _Annulus_ into the outer meatus of which it seems to be the essential support, and it constitutes the entire outer wall of the tympanic cavity. The tympanic cavity is expanded, and "_Os bullae_" has withdrawn from _Annulus_ which now for its greater extent lies isolated in the tympanic cavity connected with "_Os bullae_" by a membrane only.

FORSYTH MAJOR (1899) observed that the developing bulla apparently first pushed against the ectotympanic ("uplifting" it) and then grew completely around it. Much the same sequence has been briefly described by VAN KAMPEN (1905:678) and, more recently, by CARTMILL (1975:333).

Yet, if the ventral aspect of the petrosal plate is initially in contact with the ectotympanic, why is this relationship not maintained in later ontogeny? That is, how does the ectotympanic become 'intrabullar' when it was originally (in the ontogenetic sense)

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[1] _Lemur macaco collaris_.

'extrabullar'? Questions of this sort can only be answered through close study of a series of ontogenetic stages as the next section shows.

2.1.5.2 Development of the Ectotympanic-Petrosal Plate Relationship

Conditions in the specimens of *Microcebus murinus* are representative of the sequence of events leading up to the overgrowth of the ectotympanic by the petrosal plate, while the ten-day old *Lemur catta* (MPIH 1964/28) represents a stage shortly after the completion of overgrowth. For the purpose of the following descriptions, the tissues intervening between the petrosal plate and the ectotympanic will be said to compose the *interface* between those two structures.

The earliest state of the ectotympanic-petrosal plate interface is that seen in MPIH 1964/41, in which the RTPP has just appeared. Soft and hard tissues are arranged in the manner depicted in fig. II-9, which illustrates conditions at the level of the presumptive external acoustic meatus. The RTPP and the ectotympanic are separated by a large interval at this stage, and communicate only indirectly by means of the fibrous membrane of the tympanic cavity. Tympanic mucoid tissue occupies the space between the periosteum of the ectotympanic and the diffuse thickening of the periosteum of the auditory capsule which encloses the rudiment of the RTPP. Virtually identical conditions are found in the sectioned specimen of *Propithecus* (AI 210/211), in which the RTPP is also in the first stages of production.

Although the (now continuous) petrosal plate is only slightly larger in MPIH 1962/57, the relationship between it and the ectotympanic has become far more intimate (fig. II-11). The tympanic mucoid tissue no longer intervenes between the two periostea. In its place is a non-myxomatous, loose connective tissue which appears to be continuous with the more diffuse periosteum of the auditory capsule, rather than the denser periosteum of the ectotympanic. Nonetheless, this tissue effectively joins the two periostea at the interface.

In MPIH 1964/43, the periosteum of the petrosal plate has a very active appearance (fig. II-11), and dense aggregations of both osteoblasts and osteoclasts can be identified. It is in close contact ventrally with the somewhat less-active periosteum of the ectotympanic. Whether the two periostea are 'fused' is an open question, although the impression one has is that they are not. There is, for example, a rather sharp boundary between the denser periosteum of the ectotympanic and the more diffuse one of the petrosal plate. Further, few if any collagen fibers pass from one periosteum to the other.

Much the same picture of contiguity without apparent fusion obtains at the interface of MPIH 1964/42 (fig. II-12). The petrosal plate has not overgrown the ectotympanic at any point, although the beginning of the enclosure process can be detected in the anterior part of the interface. Here (fig. II-25), instead of simply abutting the superior surface of the ectotympanic, the petrosal plate extends a short distance around its medial side. The process of overgrowth may be visualized as a gradual extension of the ventral margin of the plate around the entire ectotympanic, until the latter is hidden from view.

In the ten-day old Lemur catta (MPIH 1964/28), overgrowth is already complete (although some further lengthening of the petrosal plate in a lateral direction could be expected, judging from the large size of the external acoustic meatus in this specimen). Note that the periostea of the ectotympanic and petrosal plate are not in contact (fig. II-13); the interface between them is occupied by connective tissue which grades into the skin forming the membranous meatus.

Earlier descriptions of the genesis of the lemuriform EPPR are thus essentially correct, in that the petrosal plate does, in fact, initially abut the ectotympanic, then grow completely around it (save for the apices of the crura). Still requiring discussion, however, is why overgrowth--rather than fusion, as in other primates--takes place. In order to deal with this problem, the tissues at the interface must be examined more closely and compared with tissues occurring in other cranial sutures.

PRITCHARD, SCOTT and GIRGIS (1956) have given a thorough account of the structure and ontogeny of cranial sutures from a histological point of view. Through the use of a variety of stains, they have exposed a wealth of microanatomical details which have been missed by other authors. Although their methods of description and interpretation have been challenged (see reviews by HOYTE 1966 and KOSKINEN, ISOTUPA, and KOSKI 1976), they are sufficiently accurate for the fairly gross analysis attempted here.

The authors define a suture (following MOSS 1954) to include note only adjoining bony edges but also the complex of soft tissues intervening between and surrounding them. Sutures per se are not regarded as having formed until a number of tissue layers have differentiated. Five such layers intervene between the bony edges of a typical suture (fig. II-15). The cambial layer is the zone of active osteogenesis and is highly cellular. The capsular layer is the periosteum which envelops the cambial layer. The middle layer is the looser, mesenchymal or cellular zone separating two adjacent capsular layers. In addition, there are two uniting layers which form connecting links of fibrous tissue between the capsular layers.

Sutures in the facial region develop somewhat differently, in their early phases, from those in the vault. Of chief interest here are the differing methods of approach of the bone edges and the formation of the middle layer. In the facial region, the bone edges approach each other through loose mesenchymal tissue. Once the edges are relatively close together, uniting layers form from this mesenchyme. In so doing, the uniting layers enclose a remnant of the mesenchyme between the advancing bone edges, and it is this latter tissue which becomes the middle layer. The bones of the vault, on the other hand, approach one another within an already-differentiated fibrous tissue, the ectomeninx. Uniting layers are derived directly from this tissue, and the portion of the ectomeninx left between them becomes the middle layer. Once the definitive sutural tissues are formed, development is thereafter essentially the same in the sutures of both vault and face.

The ectotympanic-petrosal plate interface differs in several ways from typical sutures of the face and vault. In some respects, it appears to be structurally intermediate. As in the case of vault sutures, a thick fibrous membrane, the fibrous membrane of the tympanic davity, is in close relation to the petrosal plate and the ectotympanic from the first. Unlike bones within the ectomeninx, however, the petrosal plate develops lateral to rather than within the fibrous membrane of the tympanic cavity. On the other hand, the petrosal plate approaches the ectotympanic through the tympanic mucoid tissue, which is analagous to the approach through loose mesenchymal tissue in the case of facial bones.

Of greater significance is the number of sutural-tissue layers present at the interface. Cambial and capsular layers are relatively distinct in all specimens, although the boundaries between them are not always obvious (no doubt because of the limitations of the stains employed here). However, the truly striking peculiarity of the interface is the apparent absence of the middle layer in every sectioned fetus. Thus, in MPIH 1962/57, a narrow bridge of tissue extends from the capsular layer of the petrosal plate to the capsular layer of the ectotympanic (fig. II-10). Yet this bridge is continuous with the diffuse periosteum of the petrosal plate (see above), and it does not appear to qualify as a middle layer. This interpretation receives support from conditions in older specimens of Microcebus. In these fetuses, the capsular layers of the petrosal plate and ectotympanic directly abut one another, and there is no sign of the heavily-vascularized middle layer described by PRITCHARD, SCOTT and GIRGIS

(1956) for cranial sutures (figs. II-10, II-11).

It may be argued that the absence of a middle layer is due to its inadequate visualization with Azan, but another explanation seems more plausible. PRITCHARD, SCOTT and GIRGIS (1956:77) note that in "parts of some sutures, however, where the vessels are scanty, the middle zone is inconspicuous, for the two capsular zones are very close together and partly fused." Accordingly, it is possible for the middle layer to be partly absent in certain sutures. In fetal Microcebus, however, the above description mirrors the situation throughout the ectotympanic-petrosal plate interface, not just parts of it. Blood vessels are extremely rare, and the middle layer is extraordinarily inconspicuous, if not completely absent. As noted elsewhere, it is not certain whether the periostea at the interface are indeed fused; again, one's general impression is that the capsular layers remain intact and separate.

It might also be argued that a middle layer may be formed later in ontogeny, i.e., at a stage later than that represented by M. murinus MPIH 1964/42. This would be at variance with the description of development presented by PRITCHARD, SCOTT and GIRGIS (1956), according to whom the middle layer is formed in the early phases of sutural ontogeny (however, see description of conditions in L. catta MPIH 1964/28 below).

The two uniting layers complete the complement of sutural tissues in the normal case. Here, too, conditions in M. murinus vary from the expected. It is probably safe to regard the fibrous membrane as functionally equivalent to a (medial) uniting layer, by analogy to the ectomeninx (see above). However, a (lateral) uniting layer distinct from the capsular layers at the ectotympanic-petrosal plate interface was not identifiable, for the simple reason that the periostea of the bones adjoin each other across the entire interface in specimens older than MPIH 1962/57. Close inspection of the relevant part of the interface, however, indicates that the (lateral) uniting layer, like the middle layer, is either absent or exceedingly inconspicuous.

There are some additional details of interest at the interface of the ten-day old *Lemur catta* (MPIH 1964/28). It was previously noted that the periosteum of the ectotympanic in this specimen is completely separate from that of the petrosal plate, and that the intervening space is occupied by a zone of loose connective tissue related to the membranous meatus. This tissue is not at all similar to the tissue composing the middle layer in a typical suture. Further, there is no sign of uniting layers. This may seem curious, since the fibrous membrane was counted as the functional equivalent of a (medial) uniting layer for prenatal *Microcebus*. However, the explanation for this becomes clear once the method of growth of the petrosal plate is examined. The plate actually delaminates the fibrous membrane from the periosteum of the ectotympanic as it grows around the medial surface of the latter bone (figs. II-11, II-12). Accordingly, the fibrous membrane eventually lines only the outer surfaces of the petrosal plate once overgrowth is complete (fig. II-13). The tunica mucosa, of course, runs between the ectotympanic and internal wall of the bulla, but this can hardly be regarded as a uniting layer in the usual sense.

It should be noted in passing that there is, in fact, one site in this specimen where the middle layer is present and intervenes between the ectotympanic and another skeletal element. This site is located at the point where the apex of the posterior crus articulates with the lower margin of the squamosal. Interestingly enough, this is the only position at which the ectotympanic fuses to the cranium. Nonetheless, this observation does not affect the generality of the other observations and interpretations made here, for synostosis at this position has no effect on the enclosure of the ectotympanic by the petrosal plate.

2.1.5.3 Interpretation of Observations

It may be concluded that at least part of the reason why the petrosal plate is able to grow around the ectotympanic has to do with the nature of the interface. Since the two uniting layers and the middle layer serve to bind together the periosteal capsules in a typical suture, it follows that the ectotympanic-petrosal plate interface is inherently unstable. Only the (medial) uniting layer, if the fibrous membrane may be so regarded, is well-developed; the (lateral) uniting layer and the middle layer are either absent or very poorly developed. On the face of it, this single bond is not sufficient to keep the petrosal plate and the ectotympanic in their original embryonic relationship. Instead, the petrosal plate at a certain point in its development (perhaps at the inception of the process of rapid bullar inflation) begins to glide around the ectotympanic medially, eventually covering it completely. The (medial) uniting layer, although it is eventually delaminated from the ectotympanic, may still have a 'guiding function' in directing the growth of the petrosal plate around the ectotympanic (see PRITCHARD, SCOTT and GIRGIS 1956 for analagous situations in other sutures).

Even if this explanation should be substantially correct, we may still inquire why the ectotympanic and petrosal plate fail to undergo synostosis while they abut one another. The mere absence of the middle layer, although suggestive, cannot be taken as evidence that synostosis is necessarily impossible. Unfortunately, there is as yet no satisfactory explanation of the causes of sutural fusion (see HOYTE 1966). However, the process of fusion from a histological point of view has been described by MOSS (1958). He reports that there is a "transitory tissue" in the metopic suture of the rat which differentiates within sutural soft tissues directly prior to the union of bony margins. This transitory tissue, which is described as having some of the characteristics of secondary cartilage, can either ossify directly or be replaced by bone through normal endochondral processes. Such tissue was not found within the ectotympanic-petrosal plate interface in any lemur specimen; the secondary cartilage found in the ventral enlargement of the petrosal plate in M. murinus MPIH 1964/42 (see 2.1.3.2) is completely contained within the latter's periosteum. In contrast to conditions in lemurs, transitory tissue of the sort described by MOSS (1958) was found between the ectotympanic and petrosal plate in one of the specimens of Galago senegalensis (MPIH 1967/117) used for this study (see fig. III-9). Furthermore, While these points are interesting by themselves, they also bear on our understanding of the evolution of the EPPRs found in primates. This matter will be covered in section 3.1.5, after evaluation of the development of the EPPR in modern lorises.

2.1.6 LINEA SEMICIRCULARIS

The linea semicircularis is a remarkable feature of the internal aspect of the lateral bullar wall which has been consistently overlooked in the literature. It is a continuous ridge of bone, varying in height among species, which juts into the tympanic cavity directly beneath the ectotympanic and which almost precisely follows the latter's arc of curvature across the entire internal face of the bullar wall. Its surface is, however, quite irregular (unlike that of the ectotympanic) and it sends out numerous small spines or projections along its course. The linea was present in all adult lemurs available for study, although it is low and indistinct in some (e.g., *M. murinus*). It is, together with the ectotympanic, responsible for the curved line beneath the external acoustic meatus which can be made out through the almost-translucent bullae of smaller species. An average degree of development and prominence of the linea is displayed by the postnatal specimen of *L. catta* (figs. II-8, II-13).

The linea semicircularis may be a remnant of the ventral enlargement of the petrosal plate found in fetal *Microcebus murinus*, although this is not certain. As noted earlier (see 2.1.5.2), overgrowth of the ectotympanic begins along the medial portion of the ventral enlargement (fig. II-12, II-25). It is not difficult to imagine overgrowth being completed by the growth of the medial portion alone, while the lateral portion eventually becomes the excresence here identified as the linea semicircularis. In favor of this interpretation is the close relation of the linea to the ectotympanic on the one hand and its arc-like form on the other; both of these features are characteristic of the ventral enlargement found in the earlier phases of bullar development.

It may also be noted here that the linea is not the only source of relief on the inner surface of the lateral bullar wall. CARTMILL (1975) has found that small projections also arise along the lip of the external acoustic meatus. Since these outgrowths are directed into the tympanic cavity, they might in some cases meet the linea and thus produce a broad lamella of bone beneath the ectotympanic. This might explain the source of the frequent references to 'ossified anulus membranes' in fossil lemurs (see 2.1.7).

2.1.7 'ANULUS MEMBRANE'

2.1.7.1 Introduction

There are frequent references in the paleoprimatological literature to the 'anulus membrane', a structure which supposedly connects the ectotympanic to the bullar wall in extinct and extant lemurs (WINGE 1895 [1941]; VAN KAMPEN 1905; STEHLIN 1912; VAN DER KLAAUW 1931; WOOD JONES and LAMBERT 1939; SABAN 1956-57, 1963; LE GROS CLARK 1959; VAN VALEN 1965; CARTMILL 1975; SZALAY 1975). Investigation of the development of the soft tissues of the external acoustic meatus, however, shows that there is strong reason to doubt that the 'anulus membrane exists (or, for that matter, has existed) in lemurs as a separate entity. Instead, investigators have either misidentified the membranous meatus (or parts of it) as the 'anulus membrane', or have regarded entirely different formations (the linea semicircularis and outgrowths on the meatal porus; see 2.1.6) as its ossified successors.

2.1.7.2 Observations on the Development of the Membranous Meatus

In mammals, the ectoderm surrounding the first branchial cleft becomes the membranous meatus, and thus forms the lining or external parts of all structures facing the eventual porus. In late fetal M. murinus (fig. II-7), this ectoderm is already highly differentiated, and ceruminous glands, hair follicles and other structures can easily be identified.

The ectotympanic and the tympanic membrane are situated in close proximity to ectodermal tissues throughout ontogeny; indeed, the stratum cutaneum of the tympanic membrane is a direct derivative of the skin of the meatus. One might suspect that the rim of the ectotympanic, at least, might draw away from the membranous meatus after the former is rendered aphaneric by the growing petrosal plate. In fact, this does not happen, as conditions in postnatal L. catta reveal (fig. II-13). The petrosal plate simply grows around the part of the membranous meatus in contact with the ectotympanic, thereby rendering it intrabullar as well. Accordingly, all the soft tissue intervening between the ectotympanic and internal face of the bullar wall, with the exception of the periostea, are derivatives of the membranous meatus. The only other tissue which can be considered to join the ectotympanic to the petrosal plate is the tunica mucosa, but that membrane lies entirely within the tympanic cavity.

Now, in none of the sectioned specimens is there any sign of a structure other than those already specified (i.e., the skin of the meatus, hairs, and glands). Nor is there any sign of stratification in the meatal lining, other than the divisions normally found in dermal tissue. Where, then, is the 'anulus membrane'?

SABAN (1956-57:10 and 1963:153) concludes that the intrabullar part of the membranous meatus might be the 'anulus membrane' of STEHLIN and other authors. But there is no reason to regard this part as different from the part lying outside the meatal porus, in terms of origin or fate in the adult; they are quite obviously continuous (fig. II-13). The use of the term 'anulus membrane' in this context is needless and confusing. The fact that SABAN does not specify a structure independent of the membranous meatus that could be identified as a true 'anulus membrane' nullifies the argument that it appears in a stage later than that represented by L. catta MPIH 1964/28 (ten days postnatal.

SABAN (1963) further characterizes the tissue which joins the ectotympanic to the internal aspect of the bullar wall as "cartilaginous". The skin of the meatus does not contain cartilage, although it does line the meatal portion of the cartilage of the auricle. In the adult Lemur, the meatal portion of this cartilage may extend a slight distance within the bulla, although this is doubtful. Nonetheless, there is no reason to suspect that the lateral aspect of the ectotympanic does not remain embedded within the membranous meatus, as it does in all other mammals investigated here. SABAN's description is therefore inaccurate to the extent that it conflates the membranous and the cartilaginous tissues of the meatus.

CARTMILL (1975) makes a similar mistake in his analysis of the disposition of cartilage around the porus, although he recognizes that the 'anulus membrane' (i.e., the intrabullar part of the skin of the meatus) does not contain cartilage.

A different sort of misinterpretation may be involved in references to a so-called 'ossified anulus membrane' in several fossil lemurs. What has probably been seen in these cases is either a well-developed linea semicircularis or pronounced outgrowths on the porus. The distinction is important, since these structures cannot be considered ectodermal derivatives. While this matter is of little interest in itself, the notion of the 'ossified anulus membrane' has played an important role in some conceptions of the evolution of the ectotympanic-petrosal plate relationship in strepsirhines. This topic will be further discussed in section 3.1.5.

2.1.8 OTHER TYMPANIC PROCESSES

The entoglenoid region of the squamosal is reflected medioventrally over the anterior surface of the petrosal bulla (fig. II-3), but it does not actually face on the tympanic cavity. This part of the entoglenoid stretches between the lateral wall of the foramen ovale and the Glaserian fissure (the latter being reduced to a small aperture for the exiting chorda tympani in adult Lemuriformes).

There is no alisphenoidal outgrowth which could be compared to the tympanic process of the alisphenoid of Ptilocercus or lipotyphlans. GREGORY (1920:plate XLIV) figures a 'tympanic process of the alisphenoid' for Lemur (=Varecia) varius, but the outgrowth he depicts is actually the anterior part of the petrosal plate.

The posterior part of the lateral pterygoid lamina of the alisphenoid is broadly welded to the anterior surface of the bulla in adults.

2.2 DORSAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

Lemurs, especially large ones, are distinguishes by the breadth of the dorsal wall and the great involvement of the petrosal. The epitympanic wing of the petrosal (which forms as an extension of the petrosal plate) covers the anteromedial part of the dorsal wall, while the tegmen tympani covers the anterolateral part. A narrow slit often divides the two processes in adults--all that remains of the piriform fenestra. Because the petrosal plate is recurved backwards to rest on the anterior margin of the tegmen tympani, the alisphenoid is not exposed within the tympanic cavity. The squamosal participates to a small extent by means of its epitympanic wing (fig. II-3).

2.2.1 TEGMEN TYMPANI, EPITYMPANIC WING OF THE PETROSAL, AND REICHERT'S CARTILAGE

2.2.1.1 Tegmen Tympani and Epitympanic Wing of the Petrosal

The tegmen tympani forms a substantial part of the roof of the tympanic cavity in all the sectioned specimens.

There are only slight differences in the tegmen in the series of Microcebus murinus fetuses. The reconstruction of MPIH 1962/57 (fig. II-1) depicts the tegmen as a broad tongue extending to the level of the anterior pole of the promontory. As usual, the tegmen springs from the anterolateral portion of pars canalicularis. However, instead of merely forming a short roof over the fossa incudis (as in tenrecs, for example; see 7.2.1), the tegmen projects over most of the ossicular chain (figs. II-4 to II-8).

In the two younger specimens, the tegmen is partly ossified posteromedially. It is separated from the alisphenoid anteriorly and from the side wall of pars cochlearis medially by a fairly broad piriform fenestra. The posterior part of the tegmen is deeply grooved by the facial sulcus. The medial side of the tegmen bears an oblong, shallow depression, the fossa for the tensor tympani. This fossa is incomplete dorsally because the posterior part of the piriform fenestra runs through it. The lateral margin is closely associated with the squamosal along the entire length of the developing petro-squamous suture.

There is no stapedial foramen in the tegmen of MPIH 1962/57 since this specimen lacks that vessel (see 2.4.2). There is, however, a large aperture for a plexiform vein draining from the facial sulcus into the petrosquamous sinus (fig. II-1).

In the two oldest specimens of M. murinus the tegmen is highly ossified; only its anterior and lateral margins remain cartilaginous (fig. II-2). The sulcus for the facial nerve has been converted into a semicanal by periosteal outgrowths. The stapedial artery is present in MPIH 1964/42; its foramen of exit lies close to the lateral margin of the tegmen tympani.

An epitympanic wing of the petrosal is also evident in MPIH 1964/43 and MPIH 1964/42. This wing forms concurrently with the extension of the petrosal plate from the anterior pole of the promontory. Although the original piriform fenestra has nearly been occluded in these specimens, a narrow dehisence remains between the tegmen tympani and the epitympanic wing (both of which are still actively growing). This dehisence remains in the adult as the slit associated with the anterior septum (see 2.3.2). The alisphenoid and the leading edge of the tegmen define between them a complete foramen ovale (fig. II-2).

The tegmen tympani of Propithecus sp. AI 210/211 has already been thoroughly described by STARCK (1962). It is similar to that of fetal Microcebus in all essential details.

Conditions in the postnatal specimen of L. catta (MPIH 1968/28) are nearly identical to those of the adult (see 2.2) and do not require separate description.

2.2.1.2 Reichert's Cartilage

Reichert's cartilage is a long bar, somewhat oval in cross-section, which extends lateroventrally from the crista parotica. A center of ossification, presumably for the stylohyal, is present in the distal part of the cartilage in all specimens of M. murinus. In the postnatal specimen of L. catta (fig. II-35) the proximal part of the cartilage is still unossified.

2.2.2 EPITYMPANIC WING OF THE SPHENOID

The alisphenoid of lemurs actually has a well-marked epitympanic wing in the sense that the posterior part of the bone projects backwards towards the auditory capsule. However, the wing does not participate in the roof of the tympanic cavity per se, as it overgrows the anterior part of the tegmen tympani (but it does take part in the roof of the tubal canal; see figs. II-8, II-34). The basisphenoid makes no significant contribution to this wing.

2.2.3 EPITYMPANIC WING OF THE SQUAMOSAL

The squamosal laterally bounds the tympanic cavity, the epitympanic recess, and part of the mastoid cavity in adult lemurs. It also forms part of the roof of the tympanic cavity and epitympanic recess.

The wing which forms the lateral part of the roof of the tympanic cavity and the epitympanic recess is well-developed in the oldest fetuses (fig. II-7). Posteriorly, the squamosal forms the external wall of the fossa incudis. The inflated cavern of the posttympanic process of the adult, which broadly communicates with the mastoid cavity, is in the process of formation in MPIH 1964/42 (fig. II-29).

The postglenoid process is well-marked in all specimens and is composed of secondary cartilage in the Microcebus fetuses (and is ossified in the postnatal Lemur).

2.3 PRINCIPAL SPACES AND SEPTA OF THE MIDDLE EAR

Pneumatization in peri- and postnatal lemurs produces the following series of major spaces communicating with the tympanic cavity proper: the hypotympanic sinus, epitympanic recess, and mastoid cavity. In addition, there is a small supracochlear cavity in adult stages of at least some lemurs.

Pneumatic activity greatly affects the form of the auditory bulla, which swells considerably during ontogeny and encloses an extensive hypotympanic sinus in the adult. Pneumatization of the dorsal wall and the rear of the auditory capsule, on the other hand, is much less pronounced (cf. conditions in lorises, section 3.3).

A number of fairly constant septa are also produced during the pneumatization of the bony walls of the middle ear. These are listed in table 2-4.

2.3.1 PRINCIPAL SPACES

2.3.1.1 Hypotympanic Sinus

According to SABAN (1956-57:29; 1963:166, 313-315), the hypotympanic sinus of lemurs may be subdivided into three major diverticula (D_1, D_2 and D_3). The disposition of these diverticula is illustrated for an adult L. catta in fig. II-3. Since all of them open broadly into the tympanic cavity proper, their boundaries can only be loosely defined. Diverticulum D_1 is the large excavation of the anterior bullar wall which is situated ventral to the tubal canal. Diverticulum D_2 consists of the cavern within the anteromedial process and the entire area below the promontory and the rim of the ectotympanic. Its posterior boundary is the small posterior septum which skirts the medial wall of the apertura fossulae fenestrae cochleae. Diverticulum D_3 is the small pit situated directly behind the apertura; it is bounded medially by the posterior septum and posteriorly by the rear wall of the bulla.

Strictly speaking, it makes more sense to consider SABAN's diverticulum D_3 as part of the tympanic cavity proper, since it contains the cochlear window and saccus posterior (the caudal evagination of the primordial cavum tympani which surrounds the fossula fenestrae cochleae and brings it into communication with the remainder of the tympanic cavity; see VAN KAMPEN 1905:329 and WERNER 1960b:162).

If D_3 is left out of consideration, the hypotympanic sinus as a distinct accessory space is almost absent even in the oldest fetus of M. murinus (fig. II-2). The anterior part of the petrosal plate is slightly inflated by this stage, and it is possible to predict where the rostral parts of D_1 and D_2 will lie. However, pneumatic activity has not yet significantly affected the position of the remainder of the petrosal plate, which still occupies the middle of the ventral floor of the promontory.

This finding suggests that there is an anterior-posterior gradient in the inflation of the petrosal plate in M. murinus.

This pattern is probably general among lemurs, for the anterior part of the plate is considerably expanded in the postnatal specimen of L. catta (fig. II-34), while the posterior part is not (figs. II-36, II-37).

2.3.1.2 Epitympanic Recess and Supracochlear Cavity

The epitympanic recess is not particularly large even in the oldest specimen of M. murinus (MPIH 1964/42). However, a well-marked space is evident in the postnatal specimen of L. catta (MPIH 1964/28); partly isolated within it are the facial canal, stapedial canal, and ampullar end of the lateral semicircular canal (figs. II-35, II-36).

Judging from SABAN's (1963:169) descriptions, a small supracochlear cavity is present in at least some lemurs by the adult stage. This diverticulum is a medial extension of the epitympanic recess into the dorsal (cerebral) wall of pars cochlearis, and it is of particular importance to the development of the characteristic bullar anatomy of lorises (see 3.3.1). In lemurs, however, the supracochlear cavity does not extend into the petrosal plate and thus has no effect on its architecture. A small extension of the epitympanic recess was found in L. catta MPIH 1964/28 above the stapedial canal and the fossa for the tensor tympani; this sinus occupies the same position as the nascent supracochlear cavity of young specimens of Galago (cf. figs. II-35 and III-22).

2.3.1.3 Mastoid Davity

The mastoid cavity initially develops as a posterolateral extension of the epitympanic recess. In the oldest specimens of

M. murinus it is represented only by its most anterior portion, the equivalent of the aditus ad antrum of human anatomy. In these fetuses, pneumatization has attacked the lateral wall of the auditory capsule, the squamosal, and the root of the tegmen tympani along a broad front (fig. II-29).

In the postnatal specimen of *L. catta* (figs. II-37, II-38), the aditus is continued backwards into a large space, the antrum, which is devoid of septa. This space extends posteriorly between the lateral wall of the skull (cortical bone of the petrosal) and the gyri of the lateral and superior semicircular canals. Pneumatic activity is also active along the squamosal at the site of the future posttympanic process.

In the adult lemur the mastoid davity is relatively larger than in the sectioned specimens, but in no genus is pneumatization as extensive as it is in lorises. However, CARTMILL (1975:330) points out that the pattern of pneumatization in the rare dwarf lemur *Cheirogaleus* (=*Allocebus*) *trichotis* is reminiscent of that of Lorisiformes (large mastoid cavity, hypotympanic sinus small or absent). In *Lepilemur* the mastoid cavity pneumatizes the bone between the floor of the parafloccular fossa and the external table of the petrosal, thus isolating the fossa from the sidewall of the skull. Although the posttympanic process can become relatively large through pneumatic activity (e.g., adult *Microcebus*), the petrosal plate is never inflated from the mastoid cavity (*Cheirogaleus trichotis* included, judging from CARTMILL's descriptions).

2.3.2 PRINCIPAL SEPTA

2.3.2.1 Anterior Septum

An 'incomplete' anterior septum is considered to be a general and ancient character of the lemuriform auditory region by many authors (SABAN 1963; SZALAY 1975). Although it is often compared to the 'complete' anterior septum of lorises, its ontogeny is not the same (see 3.3.2.1).

In modern lemurs, at least, the anterior septum is produced late in ontogeny along the remnant portion of the piriform fenestra (seen as the narrow dihescence between the tegmen tympani and the epitympanic wing of the petrosal; figs. II-2, II-3). In some genera (s.g., Lemur), this dihescence does not completely close, while in others (e.g., Microcebus), the tegmen tympani and epitympanic wing of the petrosal fuse together at this position.

Two processes are probably involved in the production of the anterior septum: accretion at the edges of the dihescence and the differential pneumatization of the dorsal wall of the tympanic cavity. In late fetal specimens of M. murinus (fig. II-2), the piriform fenestra is open anterior to the fossa for the tensor tympani and displays no prominences. In the postnatal specimen of L. catta, on the other hand, the margins of the tegmen tympani and epitympanic wing of the petrosal are considerably thickened (fig. II-8). This results in a prominent, divided ridge, the ventral edges of which fuse in later ontogeny to produce the definitive anterior septum.

Like most other septa, the anterior septum developes in

Table 2-4

PRINCIPAL SEPTA OF THE MIDDLE EAR
(LEMURIFORMES)

Terms Employed by SABAN (1956-57)	Terms Employed in this Study	Origin and Position
septum principal (longitudinal)	anterior septum	petrosal; forms on margins of tegmen tympani and epitympanic wing of petrosal along remnant portion of piriform fenestra parasagittally, from anterior pole of promontory to tubal canal (covers promontorial a.)
[?septum secondaire]	epitympanic crest	petrosal; on tegmen tympani runs along anterior limit of epitympanic recess (sometimes supports stapedial canal)
(petit) septum transversal	medial secondary septum	petrosal; from petrosal plate as it expands medially during pneumatization medially, from anterior pole of promontory to inner surface of medial wall of bulla (carries small vein)
(petit) septum transversal	posterior septum	petrosal; from CTPP along medial wall of apertura fossulae fenestrae cochleae (supports canal for internal carotid a.)

relation to blood vessels and nerves. In lemurs, the promontorial artery and several nerves pass along or through the dehiscence associated with the anterior septum.

2.3.2.2 Posterior Septum

A well-developed posterior septum is also characteristic of extinct and extant lemurs. It conducts the bony carotid canal to the posterior pole of the promontory and provides a medial wall for SABAN's diverticulum D_3, but its other relations are far more significant to an understanding of its ontogeny. When the posterior part of the bulla and the proximal part of the carotid canal are broken away in adult skulls in order to expose the posterior septum (fig. II-3), one immediately notes a singular association between the septum and the medial wall of the apertura fossulae fenestrae cochleae. The posterior septum occupies precisely the same position as did the original CTPP (fig. II-1).

The question arises whether the posterior septum is directly formed from the part of the petrosal plate derived from the CTPP or whether it is a new structure with a different origin. The available evidence strongly indicates that the CTPP retains, on the whole, its fetal position due to the special pattern of pneumatization of the posterior part of the hypotympanic sinus.

It was noted earlier (see 2.1.3.2) that the posterior part of the RTPP ends in a cave-like formation in the specimens of M. murinus. This formation is preserved through the stages represented by the sectioned material, and it inflates in concert with the rest of the petrosal plate (figs. II-23, II-29). In the oldest fetuses, pneumatization of the cave-like formation has created the beginnings of a diverticulum beneath the medial wall of the apertura fossulae fenestrae cochleae (which gives off the medial section of the CTPP). Although the lack of specimens of M. murinus older than MPIH 1964/42 prevents further analysis of the fate of this diverticulum, we may note that the hypotympanic sinus ends in a similar diverticulum in the postnatal specimen of L. catta (figs. II-35, II-36), and that this diverticulum is bounded laterally by the posterior septum. It appears that later pneumatization extends this diverticulum posteriorly, medially, and ventrally, but not laterally. That is, the position of the posterior septum in the ten-day old L. catta is retained in the adult (fig. II-3).

Upon combining these observations, one is led to the conclusion that this diverticulum expands by inflating into the greater part of the original CTPP. Since pneumatization involves the differential erosion and accretion of pre-existing bony surfaces, it follows that the inflating hypotympanic sinus actually splits the original CTPP into medial and lateral tables. Only the medial table is further affected by pneumatic activity; the lateral table becomes the posterior septum and does not undergo further pneumatization. This process is not unusual in the development of pneumatic spaces. Exactly the same mechanism produces the mastoid cavity, through the splitting of the cortical bone of the petrosal into inner and outer tables. An even more powerful example is the pneumatization of the petrosal plate in lorises (see 3.1.3.2).

In summary, it is suggested that the posterior septum of the adult lemur is a direct derivative of the part of the petrosal plate derived from the CTPP. It is produced by the penetration of the hypotympanic sinus into the bone of the original CTPP, which results in its eventual division into medial and lateral tables. The medial lamina is continuous with the rest of the medial wall of the petrosal plate (derived from the RTPP); the lateral lamina is not affected by pneumatization proceeding from the hypotympanic sinus, and becomes the definitive posterior septum.

2.3.2.3 Other Septa

Small septa in addition to those described above can be found within the confines of the middle ear. Two such, which appear to be fairly constant in lemurs, are the medial secondary septum and the epitympanic crest. The medial secondary septum (fig. II-3) contains a small vein which drains into the inferior petrosal sinus through the medial wall of the bulla. The epitympanic crest is a small revetement which runs along the anterior limit of the epitympanic recess and supports the stapedial canal. In lemurs with large stapedial arteries (and canals), it is not visible unless the artery is dissected away. However, it is also found in *M. murinus*, in which the stapedial artery is either tiny or completely involuted (fig. II-3).

2.4 MUSCLES, ARTERIES AND NERVES OF THE MIDDLE EAR

2.4.1 OSSICULAR MUSCLES

The fibers of the tensor tympani in the specimens of *Microcebus* arise from the length of its shallow fossa, which nearly attains the level of the anterior pole of the promontory. However, the bulk of the muscle is situated in the posterior part of the fossa, immediately in front of the foramen faciale (or, in older specimens, the proximal part of the facial canal). As usual, the muscle inserts by means of a single tendon into the processus muscularis of the malleus.

Conditions are the same in the young specimens of *Propithecus* and *Lemur*. The tensor fossa is a very prominent, high-walled trough in the adult *Lemur*, whereas it is a barely detectable depression in the adult *Microcebus*.

The tensor is supplied by a minute branch passing backwards from the otic ganglion.

In *Microcebus*, the origin of the stapedius lies at the extreme posterior end of the middle ear cavity beneath the prominence of the lateral semicircular canal. In the youngest specimens, its origin is completely open to the ventral due to the slight development of the lateral portion of the CTPP (fig. II-21). Later (fig. II-30), the part of the petrosal plate derived from the CTPP completely shields the stapedius, and its origin thus becomes intrabullar. There is a small scar at the posterolateral end of diverticulum D_3 (SABAN 1963) in the adult *Microcebus* which represents the site of origin of the stapedius.

The stapedius is entirely enclosed by the bulla in the ten-day old *Lemur* and by the cartilage of the CTPP in the specimen of *Propithecus* (fig. II-32). SABAN (1963:164) maintains that the stapedius is enclosed within a pyramidal eminence in the adult *Lemur*, but there was only a ledge of bone at the site of origin of the stapedius in the adult specimens of *Lemur catta* available for this study.

The fact that the CTPP surrounds the origin of the stapedius from the posterior in the youngest fetuses of *Microcebus* is significant, for this explains the basis for the contrasting condition described for *Tupaia* by SABAN (1963). In *Tupaia*, SABAN (1963:128 and fig. 25) found that the stapedius is enclosed within a pyrimidal canal which opens to the exterior beneath the digastric muscle. This can be correlated with the observations that the CTPP borders on the *medial* side of the stapedius in young s-ages of *Tupaia*, rendering the origin of the muscle extrabullar from the first. On the other hand, in *Microcebus* (and probably other lemurs as well; e.g., the specimen of *Propithecus*) the CTPP *encircles* the origin of the stapedius so that it lies within the confines of the presumptive middle ear cavity. Later growth essentially maintains these relationships which first appear in the prenatal development of these two genera.

The stapedius passes freely beneath the facial canal to insert by means of a tendon into the stapes. It does not occupy or arise from any part of the facial canal in the fetal and adult specimens examined.

The stapedius is supplied by a relatively large stapedial branch coming from the facial nerve. There is no element of Paaw.

2.4.2 ARTERIES

2.4.2.1 Introduction

The contributions of TANDLER (1899), VAN KAMPEN (1905) and GREGORY (1915, 1920) on the development, anatomy and evolution of the carotid pattern of lemurs have been supplemented and corrected in recent years by a number of important papers. Of particular significance are the detailed anatomical studies by SABAN (1963), BUGGE (1972, 1974) and CARTMILL (1975).

There are two contrasting patterns of carotid circulation in modern lemurs. In Cheirogaleidae, the true internal carotid and its promontorial and stapedial branches are greatly reduced in calibre compared to the equivalent vessels of other lemurs. Most of the blood from the common carotid destined for the circulus arteriosus is carried instead through another vessel, the anterior carotid (fig. II-18).

In all other lemurs, the anterior carotid is apparently absent (but see below). The internal carotid and the stapedial are well developed, but the promontorial artery is always small and may involute in some cases during ontogeny (BUGGE 1974). The vertebral arteries accordingly assume the major role in the supply of the brain (fig. II-40).

CARTMILL (1975) has made a thorough study of the anterior carotid in *Microcebus murinus*. The evidence is now quite overwhelming that the anterior carotid is the homologue of the ascending pharyngeal artery, as it has a distribution which is virtually identical to the ascending pharyngeal of man and many other mammals. Furthermore, the anterior carotid is evidently not the homologue of the medial carotid of miacids, recent carnivores, lagomorphs, and at least some rodents. The only complicating factor is that the anterior carotid has developed a very strong anastomosis with the circulus anteriosus. While no significant degree of anastomotic linkage between the ascending pharyngeal and arterial circle occurs in non-strepsirhine primates, anastomoses do occur in other mammals (notably certain carnivores). The anterior carotid is also present in lorises (see 3.4.2.2), and it too is undoubtedly the homologue of the ascending pharyngeal (see also ADAMS 1957; BUGGE 1972, 1974).

The ascending pharyngeal apparently exists in Lemur (the rameau tubaire of SABAN 1963), but it is a small vessel and has not yet been demonstrated to have a link with the circulus arteriosus.

The sectioned specimens of lemurs employed for this study are too advanced in age to shed much light on the ontogeny of the carotid circulation within the auditory region. Accordingly, only brief descriptions are required here.

2.4.2.2 Stem and Major Branches of the Internal Carotid and Anterior Carotid Arteries in M. murinus

The branches of the common carotid which pass through or around the auditory region in late fetuses do not differ significantly in their routes and connexions from those of the adult (see CARTMILL 1975).

In my specimens, the internal carotid was always bilaterally present and arose from the common carotid at the same point as the external and anterior carotids. CARTMILL (1975), however, found that the internal carotid was present only on the right side of his specimen, and arose from a short stem which also released the posterior meningeal.

In the fetal specimens, the internal carotid was a minute vessel, being no more than one-tenth the size of the anterior and external carotids (which were approximately equal in diameter). From its origin, the artery travels backwards and laterally in close association with the internal carotid nerve, entering the posterior part of the tympanic cavity from the medial (rather than the posteromedial, as in the adult). After passing over the posterior pole of the promontory, it divides into insignificant promontorial and stapedial branches of about equal size.

Although a minute, unenclosed promontorial artery was present in all specimens, in most cases its lumen was non-patent at various points along its route (cf. similar conditions in lorises; section 3.4.2.2).

The promontorial artery gradually ascends towards the roof of the tympanic cavity as it traverses the lateral wall of the promontory. Anteriorly, it leaves the anterior pole of the promontory, follows the remnant portion of the piriform fenestra for a short distance, then swings medial to the cartilage of the tube and ventral to the alicochlear commissure in order to form an extracranial anastomosis with the anterior carotid (fig. II-1).

SABAN's (1963) description of the route of the promontorial artery indicates that late fetal conditions are essentially preserved in the adult stage of M. murinus. As a result of the further growth of the anterior part of the bulla, the distal part of the artery is eventually surrounded by bone. In the adult, it issues from a canal or groove within the pharyngeal orifice of the tubal canal. Its anastomosis with the anterior carotid beneath the anterior carotid foramen, however, remains extracranial.

CARTMILL (1975) was unable to find this latter anastomosis in his specimen of M. murinus. The promontorial artery may have actually obliterated distally in this specimen, or its small size may have prevented the adequate penetration of injection mass.

The promontorial artery does not give off a branch to the pterygoid canal.

The stapedial artery was highly variable. It was entirely absent in MPIH 1962/57, distally obliterated in MPIH 1964/41 and MPIH 1964/43, and complete only in MPIH 1964/42.

In MPIH 1964/42 the stapedial travelled from its point of origin upwards through the obturator foramen of the stapes to the semicanal for the facial nerve, which it entered for a short distance. It then passes across the tegmen tympani, pierced the epitympanic crest, and left the tympanic cavity through a foramen situated near the lateral margin of the tegmen. Once outside the tympanic cavity it immediately united with the middle meningeal. The stapedial was not enclosed by bone for any part of its route (save for the epitympanic crest) and gave off no intratympanic branches.

In the two cases of distal obliteration it was possible to follow the stapedial as far as the facial sulcus, but not thereafter. It appeared to simply terminate within the mesenchyma surrounding the sulcus. In these cases, the middle meningeal received its entire supply from its anastomotic link with the ophthalmic (BUGGE 1974). According to SABAN (1963:176) the stapedial is absent only in *Phaner* among the cheirogaleids, but the fetal specimens of *M. murinus* indicates that the situation may be more variable. CARTMILL (1975) found a similar case of complete obliteration in his specimen of *M. murinus* (cf. MPIH 1962/57).

The anterior carotid is a very large vessel relative to the internal carotid in all sectioned specimens. CARTMILL (1975) has given a thorough description of its branches in the adult. The artery always lay medial to the fibrous membrane of the tympanic cavity in the sectioned specimens, and thus cannot be regarded as a vessel which 'moves' out of the presumptive tympanic cavity during development (*contra* VAN KAMPEN 1905:383 and GREGORY 1920:179). The anterior carotid-promontorial anastomosis joins the circulosus arteriosus immediately after penetrating the anterior carotid foramen. It does not possess an extracranial carotid rete (cf. conditions in lorises, section 3.4.2.2).

The fetal specimens of *M. murinus* are unfortunately too old to demonstrate how the anterior carotid comes to dominate the internal carotid-promontorial system in the supply of the anterial circle. The probable course of events, however, no doubt involves a more rapid rate of growth of the anterior carotid once it establishes its link with the circulus arteriosus. Blood destined for the brain would then be shunted along the more direct route offered by the anterior carotid.

2.4.2.3 Stem and Major Branches of the Internal Carotid Artery in L. catta and Propithecus sp.

The routes of the internal carotid and its branches in the sectioned specimens of *Lemur* and *Propithecus* are almost identical to those described for *Microcebus*. The significant difference, from a functional point of view, is the size of these vessels relative to other parts of the carotid system.

In both specimens the internal carotid is large (about two-thirds the size of the external carotid) and enters the tympanic cavity at a sharp angle. It reaches the posterior pole of the promontory, then divides into its promontorial and stapedial branches. The promontorial artery is only about one-fifth the size of the parent vessel, but it is not obliterated in any part of its route. BUGGE (1974), however, found that the distal part of the promontorial artery can be obliterated in adult *L. catta*. As in cheirogaleids, there is no vidian branch.

The stapedial artery is five times the size of the promontorial artery, and is thus equal in diameter to the internal carotid. One interesting feature found in the specimen of *Lemur*, but not in *Propithecus*, is the small dural branch given off by the stapedial adjacent to the fossa for the tensor tympani. This branch enters the cranial cavity and terminates within the dura mater (fig. II-39).

It has neither the route nor the connexions of the true ramus inferior and is evidently a neomorph.

A careful examination of the basicranium failed to reveal any connexions between SABAN's rameau tubaire (the apparent equivalent of the ascending pharyngeal) and the circulus arteriosus in either of the sectioned lemurids.

2.4.2.4 Foramina

The situation of bony foramina and canals in the different genera of Lemuriformes is quite well known (see SABAN 1963; SZALAY and KATZ 1973), and accordingly I will restrict my comments to the ontogeny of the two most important apertures, the anterior and posterior carotid foramina.

(1) Anterior Carotid Foramen

The anterior carotid foramen is easily visible in Cheirogaleidae, but the equivalent structure is completely masked in other lemurs. Despite the evident anatomical differences found in the adult stage, the anterior carotid foramina of both groups are derivatives of the foramen caroticum primitivum.

It is simpler to begin with the cheirogaleid anterior carotid foramen, since it undergoes little change from the fetal condition. The foramen caroticum primitivum is completed laterally by the alicochlear commissure (fig. II-1) in the late fetus. Concurrent with the degeneration of the cartilage surrounding the primordial foramen (fig. II-2), the anteromedial process of the bulla expands towards the aperture and provides it with a bony posterior wall.

In essence, the relations seen in MPIH 1962/42 (fig. II-2) are no different from those of the adult, in which the anterior carotid foramen is a rounded breach between the sphenoid and anteromedial process. As noted above, the foramen receives the joint vessel formed by the anterior carotid and promontorial arteries as well as the petro-occipital venous sinus.

The foramen caroticum primitivum in young stages of other lemurs has the same form as in fetal Microcebus, with the difference that it receives only the attenuated promontorial artery and becomes relatively small during later ontogeny. Also, the anteromedial process normally expands beneath the foramen, thus sealing it within the basicranium.

In the postnatal specimen of L. catta, the promontorial artery passes from the remnant portion of the piriform fenestra (fig. II-8) along the medial side of the cartilage of the tube (fig. II-34). It then becomes external for a short distance, since the anteromedial process has not yet reached full size. Thereafter, it enters a canal in the posterior part of the sphenoid which conducts it to the lateral side of the sella turcica, where it joins the circulus arteriosus (fig. II-33). This canal is the true anterior carotid foramen and the homologue of the much larger aperture found in cheirogaleids. SZALAY and KATZ (1973) have pointed out that the anteromedial process does not always completely cover the anterior carotid foramen in indriids, in which case a small perforation can be made out in the basicranium immediately in front of the bulla. CARTMILL (1975) illustrates a similar anomaly in a specimen of L. catta. He regards this aperture as evidence that a persistent anastomosis between the ascending pharyngeal (or rameau tubaire) and promontorial artery may remain into adult life. However, as noted above, there is no evidence that this anastomosis forms in non-cheirogaleid lemurs.

(2) Posterior Carotid Foramen

SZALAY and KATZ (1973) maintain that there is a certain degree of variability in the positioning of the posterior carotid foramen in Lemuriformes. In most Adapidae, Lemuridae, and Indriidae, the aperture is located in the posterocentral or posteroexternal part of the bulla, in fairly close relation with the stylomastoid foramen. In Cheirogaleidae, Lepilemur and Avahi, the foramen is posteromedial in location (and thus somewhat reminiscent of conditions in lorises; see fig. III-2).

What ontogenetic factors are responsible for this observed difference between lemurids and cheirogaleids? SZALAY and KATZ (1973) correctly identify pneumatization as an important ingredient, but it is not the only one.

It is first necessary to correct a misleading impression given by the schematic figures of strepsirhine basicrania in SZALAY and KATZ (1973:97, fig. 2). The internal carotid-common carotid bifurcation is depicted as occurring beneath the part of the basicranium, and the internal carotid as approaching the bulla from the posterior or posteromedial. In all sectioned specimens investigated by me, neither of these conditions obtained. The carotid bifurcation is located at a more anterior transverse level (fig. II-1); accordingly, the internal carotid must swing backwards rather than forwards in order to attain the posterior carotid foramen. I suspect that this curving, tangential course of the internal carotid around the posterior part of the bulla is preserved in the adult, for a shallow, medially-directed sulcus often leads into the posterior carotid foramen in mature skulls.

Now, why, in the ontogenetic sense, do lemurs and cheirogaleids differ in the manner described by SZALAY and KATZ (1973)? Two factors appear to be responsible: the growing petrosal plate and pneumatization in the hind part of the middle ear.

Although I do not have sufficient examples to prove the point for non-cheirogaleids, I suspect that the entry-point of the internal carotid is shifted in all lemurs during the development of the petrosal plate. In the younger specimens of Microcebus and in the fetus of Propithecus, the internal carotid enters the tympanic cavity from the medial side, directly opposite the apertura fossulae fenestrae cochleae (fig. II-1). In fact, the specimen of Propithecus displays the most anteromedial point of entry of the internal carotid found in any of the available strepsirhine fetuses. In this specimen, the internal carotid enters the tympanic cavity over the promontory, well in advance of the apertura fossulae fenestrae cochleae. An important observation is that early conditions correspond exactly to those of lorises in respect of the primordial entry-point of the internal carotid (fig. III-1).

In the older specimens of Microcebus (fig. II-2), the entry-point of the internal carotid has shifted. The artery now enters the tympanic cavity well behind the transverse level of the apertura fossulae fenestrae cochleae. I attribute this shift to the growing petrosal plate, over which the internal carotid must pass in order to gain the tympanic cavity. Growth of the plate evidently results in ventrolateral shifting of the artery rather in its enclosure, for even in the oldest specimen of Microcebus the posterior carotid foramen is still incomplete. Corresponding movements must take place in Propithecus (and, by extension, in other lemurs), judging from the position of the posterior carotid foramen in adult indriids (see SZALAY and KATZ 1973).

If this shift occurs in all lemurs, then one must still explain why it is that adult lemurids and cheirogaleids nonetheless differ in regard to the position of the posterior carotid foramen. I believe that the style of pneumatization of the rear part of the petrosal plate is significant here. As was explained in section 2.3.2.2, the posterior septum of the middle ear (which supports the internal carotid after it enters the tympanic cavity) is apparently produced by the splitting of the original CTPP. Pneumatic activity creates a small loculus 'within' the CTPP, and this has the effect of increasing the breadth of the hind part of the bulla. Accordingly, even though the actual position of the posterior carotid foramen is probably not further affected, it undergoes an apparent laterad shift because of the swelling of the bone medial to it (fig. II-2).

In Microcebus, this loculus does not expand to the degree seen in Lemur and other large lemurids. Thus, the breadth of the posterior wall of the bulla is relatively less, and, as a direct result, the posterior carotid foramen appears to lie more medially.

For a comparison of the development of the posterior carotid foramen in lorises and lemurs, see section 3.4.2.3

2.4.3 NERVES

The major nerves traversing the tympanic cavity are illustrated in fig. II-1.

(1) Facial (VII) Nerve

The facial nerve follows the usual course. In the younger specimens of M. murinus, it emerges into the tympanic cavity in front of the apertura fenestrae vestibuli, passes along the facial sulcus, and leaves the tympanic cavity behind Reichert's cartilage through the foramen stylomastoideum primitivum. In the older specimens (figs. II-2, II-28, II-37), the nerve travels in a more or less complete canal to the definitive stylomastoid foramen.

(2) Chorda Tympani

The chorda tympani leaves the facial nerve near the stylomastoid foramen, travels into the tympanic cavity between the ectotympanic and the squamosal, passes around the tensor tympani, then crosses over the malleolar sulcus to the Glaserian fissure. There is no element of Spence in the sectioned specimens.

(3) Internal Carotid Nerve and Deep Petrosal

The internal carotid nerve originates from the cranial cervical ganglion and accompanies the internal carotid artery into the tympanic cavity. It follows the promontorial branch of the latter artery, and meets the greater petrosal nerve in the remnant portion of the piriform fenestra. The nerve continues forwards as the deep petrosal. The internal carotid is double for most of its length (fig. II-8), and part of the medial branch of the nerve follows the promontorial artery into the cranial cavity.

(4) Greater Petrosal

The greater petrosal arises from the geniculate ganglion, passes anteriorly beneath the trigeminal ganglion (fig. II-22), along and above the remnant portion of the piriform fenestra (fig. II-8), where it meets and parallels the course of the deep petrosal.

(5) Nerves of the Pterygoid Canal

The deep and greater petrosal nerves travel out of the tympanic cavity as the nerves of the pterygoid canal. After the two meet, they issue from the tympanic cavity through the tubal canal, between the cartilage of the tube and the anteromedial process of the bulla (figs. II-33, II-34). They enter the rear aperture of the pterygoid canal under cover of the anteromedial process (in the adult), which is situated just in front of the true anterior carotid foramen.

(6) Auricular Ramus of the Vagus

A mastoid canaliculus for this nerve is formed early in bullar ontogeny in _M_. _murinus_ (figs. II-1, II-2, II-17). The canaliculus is originally situated outside of the posterior lacerate foramen (or fissura metotica), but it eventually comes to lie within the latter foramen due to the massive inflation of the bulla. In species in which the posterior part of the hypotympanic sinus is significantly inflated, a canal can sometimes be made out which carries the ramus auricularis to diverticulum D_3 (fig. II-3). The distal part of the nerve was always intratympanic in the sectioned specimens, since it travelled through D_3 in order to reach the facial canal. This condition is quite different from the majority of non-strepsirhine mammals investigated here.

(7) Tympanic Nerve and Lesser Petrosal

Considerable difficulty was encountered in the identification of this nerve. SABAN (1963:170) states that this nerve usually enters the posterior carotid foramen and follows the internal carotid to its point of bifurcation. However, the nerve which always directly accompanies the latter artery is the internal carotid nerve of the autonomic system (see above). SABAN entirely omits the internal carotid nerve from his descriptions.

One reason for confusion is that the tympanic nerve seems to be closely associated with the ramus auricularis of the vagus in almost all of the mammals investigated in this study for at least part of its route. This is different from the human condition, in which the two nerves follow separate paths from their origins within the posterior lacerate foramen.

In most of the specimens of M. murinus the tympanic nerve did not separate from the ramus auricularis vagi until they had entered D_3. Thus the mastoid canaliculus (see above) also gives entry to the tympanic nerve in these specimens (fig. II-1). In

MPIH 1964/42 and in the specimens of *Propithecus* and *L. catta*, however, the tympanic nerve separated earlier and passed through its own foramen (tympanic canaliculus) in the petrosal plate (figs. II-2, II-36, II-37).

The tympanic nerve travels through the posterior end of the tympanic cavity (fig. II-16) to the wall of the promontory beneath the apertura fenestrae vestibuli (fig. II-23). As it travels anteriorly it converges with the internal carotid nerve (fig. II-14) and enters the tympanic plexus (fig. II-35). The lesser petrosal emerges from this plexus and travels across the tegmen tympani close to or within the remnant of the piriform fenestra (figs. II-22, II-8). It then diverges anteriorly in order to pass over the cartilage of the auditory tube and finally meets the otic ganglion beneath the foramen ovale (fig. II-31).

Close inspection of the rear wall of the bulla in mature lemurs failed to reveal definite apertures which might be regarded as the tympanic canaliculus. There are several small passageways within the posterior lacerate foramen which might give entrance to this nerve, however. Another possibility is that the tympanic nerve normally enters the tympanic cavity through the mastoid canaliculus.

The foramen for the lesser petrosal cannot be seen from the ventral aspect since it lies within the tubal canal.

2.5 SUMMARY OF PRINCIPAL FINDINGS

(1) The fibrous membrane of the tympanic cavity forms the ventral wall of the presumptive middle ear cavity prior to the appearance of the tympanic processes of the petrosal, which functionally replace it.

(2) The bony ventral wall is formed by the petrosal alone. Two constituents of the petrosal bulla may be recognized, the rostral (RTPP) and caudal (CTPP) tympanic processes. The RTPP is a periosteal outgrowth of the ossified promontory, while the CTPP arises in cartilage and encircles the posterior part of the presumptive tympanic cavity. The two tympanic processes unite early in bullar ontogeny to form the petrosal plate, which becomes the definitive petrosal bulla. The CTPP does not possess its own center of ossification, but ossifies instead from the mastoid region of pars canalicularis.

(3) Although secondary cartilage is found in the petrosal plate (of late fetal M. murinus), this material does not constitute unequivocal evidence of fusion primordiale between an entotympanic and the petrosal plate. Other, more likely explanations are offered for the appearance of secondary cartilage in the petrosal bulla in fetal lemurs. The cartilage of the auditory tube and Reichert's cartilage show no sign of having incorporated entotympanic material.

(4) The ectotympanic retains the form and bony architecture ('intermediate bone') characteristic of fetal life. Only its posterior crus fuses to the squamosal and the petrosal plate; it is otherwise freely suspended within the bulla.

(5) The petrosal plate initially forms an edge-to-edge articulation with the ectotympanic, but begins to grow around it in late fetal life. This results in the definitive adult condition, in which the ectotympanic is completely surrounded by the petrosal bulla. It is suggested that this aphaneric situation of the ectotympanic obtains because of incomplete formation of sutural tissues at the ectotympanic-petrosal plate interface and the rapid and extensive pneumatization of the petrosal plate in perinatal stages. These factors appear to promote instability at the interface and permit the expanding petrosal bulla to override the ectotympanic.

(6) The 'anulus membrane' does not exist in modern lemurs, at least as a structure independent of the tunica mucosa and the tissues of the membranous meatus. It is suggested that this membrane was probably absent in ancestral lemurs as well and that the 'ossified anulus membrane' described for several fossil lemurs may simply be outgrowths of the bullar wall (such as the linea semicircularis).

(7) Outgrowths of the sphenoid and entoglenoid region of the squamosal do not actually participate in the bounding of the presumptive tympanic cavity, although they may slightly overlap the anterior part of the petrosal plate.

(8) The tegmen tympani, epitympanic wing of the petrosal, and the epitympanic wing of the squamosal appear in the dorsal wall of the middle ear. The sphenoid is excluded, although it does form the roof of the tubal canal.

(9) The piriform fenestra of fetal life is reduced to a narrow slit between the epitympanic wing of the petrosal and the tegmen tympani during ontogeny. It is often completely closed over.

(10) The effects of pneumatization on the bony walls of the middle ear are pronounced. The course of pneumatization is described and particular attention is paid to the production of the diverticula of the hypotympanic sinus and to the formation of the anterior and posterior septa. Besides influencing the position of certain foramina and the ectotympanic-petrosal plate relationship, pneumatic activity also causes the petrosal plate to migrate from its original position on the ventral surface of the promontory to one which is more medial.

(11) Findings respecting the ossicular muscles and branchings of the carotid are generally in agreement with those of other authors. The origin of the stapedius muscle is entirely intratympanic. The anterior carotid is probably the homologue of the ascending pharyngeal artery. The routes and connexions of the principal nerves passing through the middle ear are also described.

CHAPTER THREE

LORISIFORMES

METHOD OF DESCRIPTION

3.1 VENTRAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

- 3.1.1 Fibrous Membrane of the Tympanic Cavity
- 3.1.2 Cartilage of the Auditory Tube
- 3.1.3 Tympanic Processes of the Petrosal
- 3.1.4 Ectotympanic
- 3.1.5 Relationship of the Ectotympanic and Petrosal Plate
- 3.1.6 Other Tympanic Processes

3.2 DORSAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

- 3.2.1 Tegmen Tympani, Epitympanic Wing of the Petrosal, and Reichert's Cartilage
- 3.2.2 Epitympanic Wing of the Sphenoid
- 3.2.3 Epitympanic Wing of the Squamosal

3.3 PRINCIPAL SPACES AND SEPTA OF THE MIDDLE EAR

- 3.3.1 Principal Spaces
- 3.3.2 Principal Septa

3.4 MUSCLES, ARTERIES AND NERVES OF THE MIDDLE EAR

- 3.4.1 Ossicular Muscles
- 3.4.2 Arteries
- 3.4.3 Nerves

3.5 SUMMARY OF PRINCIPAL FINDINGS

3.1 VENTRAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

The gross architecture of the lorisiform ventral wall (fig. III-2) differs in two principal respects from that of lemurs. First, the bulla is compound; it consists of a petrosal plate to which the ectotympanic is firmly welded laterally. Secondly, the ventral wall is considerably swollen posteriorly by the mastoid cavity and its associated air spaces. The first difference is conditioned by sutural tissues at the ectotympanic-petrosal plate interface which differ in kind and number from those found in lemurs. The second difference is a consequence of the brunt of pneumatic activity operating in the rear of the middle ear rather than within the tympanic cavity proper.

Pneumatization also produces another difference which is not evident from external inspection of the bulla. It spreads into the actual substance of the petrosal plate, splitting it into a medial lamella (the 'true' medioventral wall) and a lateral lamella (the so-called 'longitudinal septum').

There is no ontogenetic evidence for an entotympanic element. Muscular processes are always small.

3.1.1 FIBROUS MEMBRANE OF THE TYMPANIC CAVITY

The use of Cresyl Violet and Klüver-Barrera on the youngest lorisiform specimens prevents adequate description of the fibrous membrane, since these stains visualize fibers very poorly. In the

Table 3-1

LORISIFORMES

SPECIMENS		No.	CRL[1]	HL[2]	ST[3]	PS[4]	STAIN(S)
GALAGINAE							
Galago demidovii							
I.	Fetus	MPIH 102	26.0	12.0	10	cross	Cresyl Violet, Klüver-Barrera
II.	Fetus	MPIH 125	26.5	13.0	10	cross	Klüver-Barrera
III.	Near-Term Fetus	MPIH 120	37.5	18.0	10	cross	Cresyl Violet
IV.	Newborn	MPIH 124	45.0	24.0	10	cross	Cresyl Violet
Galago senegalensis							
V.	Newborn	MPIH 1962/40	--	--	15	cross	Azan
VI.	10 Days Postnatal	MPIH 1967/117	--	--	10	sagittal	Azan
LORISINAE							
Loris tardigradus							
VII.	Near-Term Fetus	MPIH 1666	52.0	24.5	20	cross	Azan, PAS-AB

[1] Crown-rump length (in mm)

[2] Head length (in mm)

[3] Section thickness (in mμ)

[4] Plane of sectioning

NOTES ON SPECIMENS

Specimens I-IV were gathered from the uteri of pregnant females collected at Muhulu, Zaire (see STEPHAN 1958). Specimens V-VII were born in captivity at the Max-Planck-Institut für Hirnforschung.

Adult skulls available for study included several specimens of *Galago senegalensis*, *G. crassicaudatus*, and *Loris tardigradus* (all from the collections of MPIH).

remaining, Azan-stained specimens, bullar development is far advanced and the fibrous membrane is not easily distinguished from periosteal tissues clothing the petrosal plate. However, a dense strand of cells in MPIH 125 (fig. III-3) has the right relations for a fibrous membrane, and in any event the membrane is clearly present in the fetal specimen of *Galago senegalensis* investigated by KANAM and KANAGASUNTHERAM (1964:114, fig. 4). Although conditions are by no means as clear as they are in the *Microcebus* material (see 2.1.1.1), it appears that the RTPP originates adjacent to, and not within, the fibrous membrane as well (fig. III-7).

3.1.2 CARTILAGE OF THE AUDITORY TUBE

The cartilage of the tube presents no peculiarities. In older specimens (fig. III-1) it has the form of a long bar of cartilage with folded margins. No accessory cartilages were found in any of the sectioned specimens.

The alisphenoid covers the cartilage of the tube dorsally, and, as in lemurs, the tubal canal is completed ventrally by a lamina of the petrosal plate in late ontogeny (fig. III-20).

3.1.3 TYMPANIC PROCESSES OF THE PETROSAL

3.1.3.1 Introduction

The auditory bulla of lorises is composite, in the sense that it consists of a broadened ectotympanic fused to the lateral aspect of a well-developed petrosal plate (fig. III-33). In this feature, the lorisiform bulla is grossly like that of all other living non-lemuriform primates.

Unlike the case with lemurs (see 2.1.4.1), the ontogeny of the lorisiform bulla has attracted little attention. Instead, interest has generally focused on the significance of the phaneric ectotympanic to the unravelling of strepsirhine evolution (see 3.1.5.4).

The earliest interpretation regarding the construction of the bulla held that it was entirely formed by the ectotympanic (WINGE 1895 [1941]:335). Indeed, WINGE used the shape of the ectotympanic ('ring-shaped' vs. 'bowl-shaped') as the single major character for dividing his concept of the Lemuridae into Lemurini and Nycticebini (essentially equivalent to the modern infraorders Lemuriformes and Lorisiformes).

The true construction of the bulla was determined by FORSYTH MAJOR (1899:988):

> In a young Nycticebus...it is to be seen that the median part of the bulla is, as in Malagasy Lemurs, formed from an appendage of the periotic, which becomes co-ossified with the annulus; in the specimen exhibited the suture between them is distinctly visible. The annulus, in its turn, no longer plays the passive part that it does in Malagasy Lemurs, but grows out laterally so as to form the lateral part of the tympanic cavity, which, however, never reaches the dimensions it has in Malagasy Lemurs.

VAN KAMPEN (1905:665-666) confirmed FORSYTH MAJOR's description on the basis of early postnatal specimens of lorises, and added details on the ontogeny of the middle ear cavity (fig. III-31). He also observed that the mastoid area contributed to the bulla.

VAN VALEN (1965:144) believed that two separate petrosal outgrowths might be involved in the production of the lorisiform bulla in addition to the ectotympanic. He stated that an 'apparent suture' is detectable in the region of the posterior carotid foramen between the bulla proper and the mastoid in young specimens of *Galago*.

The only other direct contribution to the question of the ontogeny of the bulla is that of RAMASWAMI (1957), who studied skull development in a series of alizarin-stained young specimens of *Loris tardigradus*. He apparently considered the entire petrosal contribution to the bulla to be an outgrowth of the mastoid ('mastoid extension', fig. III-30), although precisely what he meant by this is not clear.

Thus, as in the case of lemurs (see 2.1.3.1), the specific contribution of the mastoid region to the bulla is ambiguous. My findings are that both a rostral (RTPP) and a caudal (CTPP) tympanic process of the petrosal contribute to the lorisiform bulla.

3.1.3.2 Structure, Relations and Development of the Petrosal Plate

(1) Conditions in Specimens of *Galago demidovii* and *G. senegalensis*

The relations of the two tympanic processes of the petrosal differ slightly from those found in the sectioned specimens of *Microcebus*, but the overriding similarities are quite manifest (cf. figs. II-1 and III-1). In *G. demidovii* MPIH 120 (fig. III-1), an arc of low trabeculae crosses the ventral surface of the promontory and terminates at the level of the apertura fossulae fenestrae cochleae. This ridge is the clear homologue of the RTPP identified in fetal specimens of *Microcebus*; as in this genus, it is a periosteal outgrowth which forms once the ventral surface of the promontory is ossified. Posterior to the site of termination of the RTPP is a small, mostly-cartilaginous rampart which communicates medially with a massive, hood-like projection of cartilage covering most of the posterior part of the tympanic cavity. These cartilaginous prominences are regarded together as the equivalent of the cartilaginous CTPP of fetal *Microcebus*. However, there are differences in details of CTPP construction in *Galago* which require further comment.

In fetal stages of *Microcebus murinus*, the CTPP is a unit having medial, posterior and lateral sections. The medial and posterior parts form on the medial wall of the apertura fossulae fenestrae cochleae (MWF, processus recessus of embryology) and the adjacent anteroventral surface of the pars canalicularis, while the lateral part is elaborated from the posterior continuation of the crista parotica. This lateral part is negligible in *Microcebus* until bullar ontogeny is well advanced (although this is not true of all lemurs; cf. *Propithecus* sp. AI 210/211, section 2.1.3.2). The auricular ramus of the vagus (sometimes with the tympanic nerve) pierces the CTPP at the intersection of the medial and posterior sections, but the internal carotid artery and nerve remain free of the CTPP until late in the ossification of the ventral wall of the tympanic cavity.

In the case of *Galago*, we may distinguish posterolateral and medial sections of the CTPP. Again, these sections are morphological subdivisions and are employed for descriptive purposes only. The posterolateral section is much the later and occupies the same area as the posterior and lateral sections of the cheirogaleid CTPP (fig. III-12; see also fig. II-1). The medial section of the cartilaginous CTPP in *Galago* is somewhat different from that of *Microcebus* in that it is originally restricted to the area where the floor of the promontory grades into the processus recessus[1] (figs. III-10, III-11). It forms the anterior boundary of a long incisure which accommodates the internal carotid artery and nerve, a small vein, auricular ramus of the vagus, and the tympanic nerve. This incisure becomes a foramen after the medial and posterolateral sections of the CTPP are united by a narrow bridge of cartilage (figs. III-1, III-18). As in *Microcebus*, the RTPP and CTPP coalesce early in bullar ontogeny in order to form a petrosal plate.

On the whole, the differences between *Microcebus* and *Galago* in the initial stages of bullar development are minor. In both genera the RTPP arises as a periosteal outgrowth of the ventral surface of the promontory. The CTPP has a slightly different structure in each form and different relations to the nerves and blood vessels entering the posterior part of the presumptive tympanic cavity.

Galago demidovii MPIH 102 and MPIH 125

The RTPP is absent in these two specimens since the entire auditory capsule is still cartilaginous (fig. III-3). The medial part of the CTPP is represented by a small outgrowth which is composed of cartilage younger than that making up the rest of the cochlear floor (fig. III-10). However, the medial part is continuous with surrounding cartilage, and it is highly unlikely that it chondrifies independently. The bridge uniting the medial and posterolateral parts of the CTPP has not yet formed. The posterolateral part is very large (fig. III-12); it arises at least as early as the 19 mm. CRL stage in Galago senegalensis ("mastoid process" of KANAGASUNTHERAM and KANAN 1964).

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[1] The processus recessus arises rather late in the development of the auditory capsule. It is not present in the 19 mm. CRL stage of *G. senegalensis* according to KANAGASUNTHERAM and KANAN (1964).

Galago demidovii MPIH 120

The major features of the RTPP and CTPP have already been described for this specimen (see above).

The trabeculae of the RTPP are continuous with periosteal splints on the medial section of the CTPP (figs. III-1, III-15). The RTPP and CTPP may now be regarded as a single unit, the petrosal plate (cf. Microcebus, 2.1.3.2).

The arc of the RTPP section of the petrosal plate roughly corresponds to that of the ectotympanic (fig. III-1), but the two are not yet in intimate contact (fig. III-7). The relationship of the RTPP to the soft tissues lying between the ectotympanic and the ventral surface of the promontory is difficult to determine because of the stains employed. Superficially, the RTPP and dorsal surface of the ectotympanic appear to be embedded in a very thick mass of connective tissue (fig. III-7), but close inspection of the cells of this tissue show that it is not homogeneous in structure. Surrounding the trabeculae are osteoblasts and mesenchymal cells which constitute the cellular components of a definite, if diffuse, periosteum continuous with that of the promontory. The periosteum is bounded medially by a dense band of spindle-shaped cells which must represent the fibrous membrane of the tympanic cavity. On this interpretation, the trabeculae of the RTPP would then originate adjacent to but not within the fibrous membrane.

The cartilage of the medial section of the CTPP is partly encased in periosteal splints and is calcified in some areas. It is the only portion of the MWF which is still cartilaginous, which is to be expected on the basis of its late appearance (see MPIH 102 and 125). This medial cartilage is apparently not replaced by bone in the usual manner of endochondral ossification. Instead, the cartilage is calcified and removed, leaving a cavity between the periosteal splints which later becomes a small diverticulum of the middle ear (see descriptions of MPIH 124 and 1962/40). While not a precise ontogenetic equivalent of the cave-like formation of the RTPP described for fetal specimens of Microcebus (see 2.1.3.2), this diverticulum marks the structural boundary between the sections of the petrosal plate derived from the RTPP and CTPP.

The posterolateral section of the CTPP which is now joined to the medial section by means of the cartilaginous bridge described earlier (fig. III-1), is partly ossified along its free margin (fig. III-19). The sections of the CTPP do not have their own centers of ossification, but are instead ossified from adjacent parts of the auditory capsule.

Galago demidovii MPIH 124 and G. senegalensis MPIH 1962/40

Although these two specimens are from different species, they show equivalent conditions of the petrosal plate and may be described together.

The petrosal plate, which has grown an extraordinary amount relative to its size in the near-term fetus (MPIH 120), is concave laterally and closely surrounds the greater part of the circumference of the ectotympanic (figs. III-20, III-21). However, there are no signs of actual fusion between the two at this stage.

The part of the petrosal plate derived from the RTPP is situated as before in the middle of the ventral surface of the promontory, and it displays a marked dorsoventral gradient in the activity of its periosteum. The bone of the dorsal moiety of the plate is thin, somewhat lamellated, and closely invested by its periosteum, which has a relatively inactive appearance. In contrast, the ventral moiety, situated directly above the ectotympanic, consists of massive trabeculae of young woven bone encased in a highly active, thick periosteum. The architecture of the actively-growing lower segment of the petrosal plate may be compared to the ventral enlargement described for the fetal specimens of Microcebus (fig. III-8). However, there is no sign of the secondary cartilage found at this position in the oldest specimen of Microcebus (MPIH 1964/42).[1]

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[1] However, considering the rapidity with which the petrosal plate grows, it would hardly be surprising if secondary cartilage were formed at some point (perhaps at a stage not represented here).

The petrosal plate has grown out from the anterior pole of the promontory and now possesses a definite anterior projection. The construction of the anterior projection at this stage is simpler than that of equivalent stages of Microcebus; an anteromedial process is completely lacking and the superior wing is no more than an inconspicuous ledge (see 3.2.1). However, the lip of bone forming the ventral floor of the developing tubal canal is well-developed (fig. III-20).

The petrosal plate descends in height from anterior to posterior. There is a wide but shallow diverticulum opening anteriorly into the middle ear cavity in the region of the MWF (fig. III-22). This diverticulum is situated in the same position as the periosteal splints which surrounded the medial section of the CTPP in the near-term fetus (fig. III-17). Evidently, these splints remain after the destruction of the cartilage of the medial section of the CTPP and become incorporated within the petrosal plate. The resulting diverticulum does not become part of, or communicate with, the medial accessory cavity (see description of MPIH 1967/117). Instead, it remains within the tympanic cavity proper as a small pocket ventromedial to the fossula fenestrae cochleae. The internal carotid traverses the lateral wall of this diverticulum upon entering the tympanic cavity from the medial accessory cavity in the adult (fig. III-2, III-22).

Close inspection of the petrosal plate in the area of the posterior carotid foramen in both neonatal specimens indicates to me that VAN VALEN's (1965:144) "apparent suture" is only a depression in the wall of the plate. The available specimens of Galago demonstrate that the two constituents of the petrosal plate--the RTPP and CTPP--become a single lamella without the production of any sutural tissues.

The part of the petrosal plate derived from the CTPP (i.e., posterior to the diverticulum mentioned above) is completely ossified in both specimens. Its free margin presents a ventral enlargement where it is in close association with the posterior crus of the ectotympanic (fig. III-22). The large foramen for the internal carotid and the various nerves entering the posterior part of the tympanic cavity has become reduced in size and subdivided as a result of the further development of the plate.

The origin of the stapedius muscle is accommodated on a prominent ledge on the tympanic surface of the plate (fig. III-24). The petrosal plate forms, at its juncture with the squamosal and ectotympanic, a complete stylomastoid foramen.

Galago senegalensis MPIH 1967/117

There are two striking features of the petrosal plate in this specimen: it has begun to fuse, along its margin, with the ectotympanic (see 3.1.4); and it is in the process of splitting into medial and lateral lamellae.

Since the splitting is connected with the process of inflation of the middle ear cavity, it is necessary to introduce some aspects of pneumatization at this point (see also 3.3).

VAN KAMPEN (1905:670 [trans.]) was the first to appreciate the significance of pneumatization to the production of the bulla in lorises:

> The further development of the bulla now diverges from the Lemuridae. In a somewhat older Galago galago Schreb....the cavity in the mastoid process has proceeded anteriorly into the posterior part of the bullar lamella, which is here inflated and cavernous. It is clear how the definitive condition arises from this. This cavity in the bullar wall need only progress further anteriorly and expand into the pars petrosa. In this way the wall of the bulla is split into two lamellae, the one corresponding to the definitive wall of the bulla and the other to the septum.

All lorises possess this (longitudinal) septum, which is considered to be one of the chief distinguishing marks of the lorisiform auditory region (fig. III-2). The longitudinal septum forms a complete partition between two cavities, the tympanic and the medial accessory. The medial accessory cavity is simply an empty chamber (or series of chambers subdivided by small septa) situated between the longitudinal septum and the medial wall of the bulla. As VAN KAMPEN noted, it is produced by the pneumatization of the bone of the petrosal plate. However, he thought that pneumatization proceeded from the mastoid cavity alone, which is not the case. The anterior part of the petrosal plate is pneumatized separately from the supracochlear cavity (see 3.3 and figs. III-26, III-2), a pneumatic space which excavates the dorsal part of promontory, arcuate eminence, and, eventually, the petrosal plate.

The medial accessory cavity is thus a further extension of the mastoid and supracochlear cavities, which are in turn extensions of the epitympanic recess and tympanic cavity. The mastoid and supracochlear cavities do not necessarily meet and form a single large cavern as in Galago crassicaudatus (fig. III-2).[1] In Loris, for example, the petrosal plate is not always split completely in two, and as a consequence the extensions of the mastoid and supracochlear cavities do not meet. In this case one may designate anterior and posterior medial accessory cavities.

A final remarkable feature of the pneumatization of the petrosal plate is that it leaves the lateral lamella (or longitudinal septum) virtually untouched. The form, curvature and position of the lamella in the adult is essentially the same as that of the entire petrosal plate in the newborn. In effect, only the medial surface of the plate is affected by the pneumatization process.

In MPIH 1967/117 the mastoid cavity is already large and it has just begun to pneumatize the petrosal plate from the rear (fig. III-28). The supracochlear cavity is highly developed, and it may be traced across the roof of the pars cochlearis to the anterior projection of the petrosal plate (figs. III-27, III-26). The anterior process of the bulla is also in evidence at this stage; in contrast to lemurs, it is formed through the pneumatization of the plate by the supracochlear cavity.

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[1] CARTMILL (pers. comm.) has found that the mastoid and supracochlear cavities do not, in fact, meet in some specimens of G. crassicaudatus examined by him. This indicates that there is probably much individual variation within species for this feature.

(2) Conditions in Loris tardigradus MPIH 1666

The late fetus of Loris tardigradus displays a degree of petrosal plate development comparable to the neonates of Galago (figs. III-32, III-33). The mastoid and supracochlear cavities are in evidence, but neither has expanded into the plate. There are no signs of fusion with the ectotympanic.

There are a few minor differences in architecture. Perhaps the most obvious is the lack of a diverticulum beneath the apertura fossulae fenestrae cochleae (fig. III-33), such as that seen in Galago. Accordingly, it is not possible to make a structural division between the RTPP and CTPP at this stage.

RAMASWAMI (1957) illustrates the auditory region of a 27 mm HL specimen of L. tardigradus (fig. III-30), but the petrosal plate of this fetus is not as well-developed as that found in the 24.5 mm HL specimen used for this study. RAMASWAMI calls the entire petrosal contribution to the bulla the "mastoid extension", but this term is inappropriate to the extent that it conveys the impression that the bulla is solely a mastoidal outgrowth.

Another complication is that RAMASWAMI (1957:35) claims that a "mastoid process" is absent in his young specimens of Loris. This should not be taken to mean that a CTPP is not formed in cartilage in this genus, for RAMASWAMI illustrates a large rampart of cartilage posterior to the fossula fenestrae cochleae in his reconstruction of a 22 mm HL specimen (1957:32, fig. 10). This rampart is identified as the 'crista parotica', but if the reconstruction is correct it has a most unusual form in that it has only a very narrow area of attachment to the auditory capsule. Since RAMASWAMI does not provide cross-sections of the relevant area the accuracy of his figure cannot be checked. However, conditions in MPIH 1666 indicate that it is exceedingly doubtful that Loris departs in any significant way from Galago in the origin of the tympanic processes of the petrosal.

3.1.4 ECTOTYMPANIC

3.1.4.1 Structure, Relations and Development

The ectotympanic expands laterally in all lorises during ontogeny, although to different degrees in different species (see SABAN 1963:262-264). A broadened ectotympanic is another of the features which distinguish contemporary lorises and lemurs.

Initially, the ectotympanic is anular in form (fig. III-1), as in young stages of all mammals. The similarity between prenatal Microcebus and Galago in regard to the shape of the ectotympanic is obvious and does not require detailed comment.

By the time of birth (fig. III-8), the ectotympanic is noticeably wider than in any of the sectioned lemurs. The ectotympanic increases in breadth through the deposition of bone around its lateral circumference; there is medial deposition as well, but only to a minor degree. The ectotympanic reaches its final diameter by the juvenile stage.

Fusion of the apices of the crura with the squamosal is initiated at the same time as fusion with the petrosal plate (i.e., postnatally; see 3.1.5).

The ectotympanic is mostly composed of intermediate bone in the adult, but it differs in one important structural respect from the ectotympanic of adult lemurs (see 2.1.4.1). In lemurs, the ectotympanic is wholly formed of intermediate bone. In lorises, however, lamellated bone is laid down on the lateral surface of the ectotympanic (which is otherwise composed of intermediate tissue) after it fuses with the petrosal plate. The latter set of conditions is illustrated in fig. III-29.[1] The contrast between the intermediate bone of the (original) ectotympanic and the lamellated bone of the petrosal plate is manifest. Despite the appearance of the illustrated section, it should not be concluded that the lamellated bone applied to the lateral surface of the ectotympanic element is derived from the petrosal plate *per se*. Ontogeny quite definitely shows that the plate does not grow around the ectotympanic in lorises, but instead solidly fuses with its medial aspect (see 3.1.5). The only possible interpretation is that the periosteum investing the lateral surface of the ectotympanic becomes competent to produce lamellated bone *after* ectotympanic-petrosal plate synostosis. As a direct consequence of the production of new bone at this site, the boundary between the ectotympanic and the petrosal plate is completely masked. Nonetheless, it is interesting to note that appropriate histological methods can still reveal the position of this boundary in the mature stage. In this context, it would be useful to possess information on the architecture of bullar bone in adult Loris. SABAN (1963:262) argues, and CARTMILL (1975:329) concurs, that the anterior crus of the ectotympanic is not exposed externally (i.e., is covered by the petrosal plate; cf. lemurs). Such a conclusion contradicts the available evidence on the development of the ectotympanic-petrosal plate relationship in lorises (see 3.1.5), although I have had to infer final conditions for Loris on the basis of a single sectioned specimen.

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[1] Although the figure displays conditions in an adult *Tarsius bancanus*, I have seen precisely the same differences in bony architecture in a sectioned adult *G. senegalensis* (not illustrated here).

3.1.4.2 Inclination of the Ectotympanic

Values for the angle of inclination in some young stages of lorises are listed in table 3-2. As in the case of lemurs (see 2.1.4.2), it is not possible to infer a great deal about ectotympanic rotation on the basis of such a limited sample. However, I suggest that the final orientation of the ectotympanic is probably achieved relatively earlier in ontogeny in lorises than in lemurs. The ventral hinge (between the petrosal plate and the ectotympanic) must lose its ability to move once synostosis is initiated (beginning at ca. 10 days after birth in G. senegalensis). Since very little pneumatization occurs within the tympanic cavity after birth (see 3.3.1), inflation ought not to have any significant effect on the position of the ectotympanic.

Measurement of the angle of inclination in a single adult specimen of G. senegalensis (ca. 50°) indicates that the final disposition of the ectotympanic is attained around the time of birth, since nearly the same value is found in the sectioned neonatus (cf. conditions in M. murinus, section 2.1.4.2).

Table 3-2

INCLINATION OF THE ECTOTYMPANIC IN YOUNG LORISIFORMES

Specimen No.	Angle of Inclination L	Angle of Inclination R	Average Inclination
Galago demidovii			
MPIH 102	38°	39°	38.5°
MPIH 125	43°	44°	43.5°
MPIH 120	27°	30°	28.5°
MPIH 124	44°	43°	43.5°
Galago senegalensis[1]			
MPIH 1962/40	51°	52°	51.5°
MPIH 1967/117	--	--	--
Loris tardigradus			
MPIH 1666	48°	52°	50.0°

[1] Inclination values for MPIH 1967/117 could not be determined because this specimen was cut sagittally.

For computation of the angle of inclination, see note accompanying table 2-2.

3.1.5 RELATIONSHIP OF THE ECTOTYMPANIC AND PETROSAL PLATE

3.1.5.1 Introduction

In the adult loris, synostosis of the phaneric ectotympanic with the petrosal is so complete that it is difficult to trace the positions of the sutures which originally separated them. The ectotympanic does not send out a prominent medial flange (see 3.1.4), so the crista tympanica is an approximate guide to the site of the obliterated ectotympanic-petrosal plate suture. Unfortunately, the crista is difficult to locate by external examination, except in those forms with nearly-translucent bullar walls (e.g., the smaller species of Galago). However, the difference between the texture of the bone of the petrosal plate and that of the ectotympanic is clear enough in sectioned material (see fig. III-29).

A deep groove at the site of the stylomastoid foramen indicates the original division between the posterior leg of the ectotympanic and the petrosal plate (fig. III-2). The apices of the ectotympanic crura are completely fused with the squamosal, and their precise contribution to the superior wall of the external acoustic meatus cannot be determined in the adult. Perhaps the rugose areas found on the medial margin of the superior meatal wall are ectotympanic in origin.

There are no previous descriptions of the ontogeny of the ectotympanic-petrosal suture, and so a detailed study is presented below.

3.1.5.2 Development of the Ectotympanic-Petrosal Plate Relationship

In the course of description of the specimens of *M. murinus* (see 2.1.5.2), it was noted that the growing petrosal plate rapidly forms an edge-to-edge articulation with the ectotympanic. This articulation does not become a true suture, with a full completion of sutural tissues. Instead, it simply represents a transitory approximation of bone territories which is modified in the late fetus and newborn by petrosal enclosure of the ectotympanic. In contrast, in *Galago* and other lorises this edge-to-edge articulation becomes a true suture, and the original relationship of the ectotympanic and petrosal plate is preserved throughout bullar ontogeny.

The early development of the EPPR cannot be usefully discussed here because of the stains used on the specimens of *G. demidovii*. However, sutural tissues are elaborated at least by the time of birth, if not well before, in *G. senegalensis.* In MPIH 1962/40 (fig. III-8a), all five intervening layers and two uniting layers can be identified (see PRITCHARD, SCOTT and GIRGIS 1956). The cambial layer of the rapidly-growing petrosal plate is extremely thick and contains osteoblasts in various stages of differentiation. The cambial layer of the ectotympanic is thin relative to that of the petrosal plate and appears to be less active. The middle layer cannot be sharply distinguished from adjacent capsular layers with Azan staining, although it is definitely present (cf. fig. II-11). The middle layer is somewhat easier to identify in the representative of *L. tardigradus* (fig. III-8b). Thick, fibrous strata bind the whole sutural complex together medially and laterally. The medial stratum (or uniting layer) is apparently the fibrous membrane of the tympanic cavity, for no divisions appear within this layer under bright field or polarized light other than the pseudolamellar stratification commonly found in dense connective tissue sheets. However, an independent lateral uniting layer is obviously present.

Thus, in every essential detail the tissues between the ectotympanic and petrosal plate conform to the true sutural tissues of PRITCHARD, SCOTT and GIRGIS (1956).

The next event in the development of the ectotympanic-petrosal plate suture is synostotic union of bone territories. Fortunately, the initial phase of fusion is represented in the postnatal specimen of G. senegalensis (MPIH 1967/117). The uniting layers of the suture are still distinct, but the five intervening layers have altered radically (fig. 9). Within the suture itself, the individual capsular and middle layers have been replaced by (or have differentiated into) another type of tissue of a unique sort. In the dorsal part of the suture, this tissue is continuous with the trabeculae of the petrosal plate and the more organized bone of the ectotympanic. It conforms closely in its architecture to the bone of the petrosal plate (which is of the woven type at this stage), save for the larger size and irregularity of its lacunae. This area grades ventrally, without any sharp boundary, into a looser, highly-cellular, pale-staining zone. While this latter material slightly resembles cartilage (cf. Reichert's cartilage in fig. III-9), it is distinctly less organized in appearance than either primary or secondary cartilage. However, it does bear a resemblance to the "intermediate secondary cartilage" described by MOSS (1958). This intermediate cartilage is considered to be of a lower order of differentiation than the "definitive secondary cartilage" of the postglenoid process or the palatine bones. Most importantly, intermediate secondary cartilage transforms directly into bone without any intervening phase of endochondral replacement. The bone of the dorsal part of the ectotympanic-petrosal plate suture grades directly into the intermediate secondary cartilage of the ventral part of the suture, indicating that synostosis is effected metaplastically (as in the metopic suture of the rat; see MOSS 1958).

3.1.5.3 Interpretation of Observations

The ectotympanic-petrosal plate suture presents no important problems, as it matures like other cranial sutures which eventually obliterate. While pneumatization appears to have some role in the production of the EPPR characteristic of lemurs, its effects in lorises seem to be neutral. As noted in section 3.1.3.2, the petrosal plate is split into two lamellae, only the medial of which experiences further pneumatization. The lateral lamella, and therewith the ectotympanic, retain their fetal positions. Accordingly, although pneumatization has pronounced effects on the petrosal plate, it does not proceed in a way which could disturb the edge-to-edge articulation of the latter with the ectotympanic.

The ectotympanic is in contact throughout ontogeny with tissues destined to become the membranous meatus, but presumptive meatal tissues never intervene between the ectotympanic and petrosal plate because they retain their fetal positioning. If a linea semicircularis (see 2.1.6) forms in lorises, it cannot be identified in the adult (see fig. III-29).

3.1.5.4 Production of the EPPR in Ancestral Strepsirhines

Now that ontogenetic data on the maturation of the EPPR have been presented for both lemurs and lorises, we may turn to the matter of how the different expressions of the EPPR could have arisen in ancestral strepsirhines. This question is explored at length elsewhere (MACPHEE 1977), and only its more significant aspects need be covered here.

Paleoprimatologists have long argued over which of the two character states of the EPPR is the older, and the degree to which the EPPR is a useful marker of phyletic relationships (among more recent papers, see SZALAY 1975; CARTMILL 1975; GINGERICH 1976). However, when a given state arose is not the only significant problem in character phylogeny. How it arose (i.e., what biological processes are required in order to produce it) is also important.

Few authors have concerned themselves with deducing a plausible mechanism which could account for the production (and evolution) of the EPPRs found in primates. GREGORY (1920) and HERSHKOVITZ (1974) relate exteriorization of the ectotympanic to the lateral displacement of its crura, occasioned by an increase in brain size during primate evolution. It is not in dispute that expansion of the braincase plays some role in the positioning of the ectotympanic, as does the bulla (FORSTER 1925; and sections 2.1.4.2, 3.1.4.2). However, it is certainly insufficient to ascribe the contrasting conditions of the EPPR seen in modern lorises and lemurs to the growth of the neurocranium alone. Some other factor must be involved as well.

CARTMILL (1975) suggests that this factor might relate to the mechanical efficiency of the middle ear. In essence, he argues that the total reactive impedance of the middle ear could be reduced in smaller lemurs if the relatively large tympanic membrane were situated close to the bullar wall, instead of a distance from it (as in larger lemurs). This would have the effect of increasing bullar volume, and would thus decrease part of the stiffness component of middle ear impedance (see appendix I).

It is difficult to see how such a slight difference in the disposition of the membrane could have much effect on bullar volume. However, some functional basis for EPPR differences may nonetheless exist, and the matter deserves further research. In order to make real headway into an understanding of the properties of the strepsirhine tympano-ossicular-cochlear system, we require physical and anatomical data of the sort presented in such exquisite detail by WEBSTER (1961, 1962, 1975) for heteromyid rodents.

Many authors have suggested that the intrabullar relationship could have given rise to the extrabullar one through the ossification of the 'anulus membrane' (see especially VAN VALEN 1965). In my view, this explanation can be wholly discounted. The 'anulus membrane' is merely a part of the membranous meatus (see 2.1.7), and it is highly unlikely that the latter could ossify except in a pathological context. It is not impossible that an hypertrophied linea semicircularis could fuse with the ectotympanic, or meet excrescences developed on the meatal lip (see 2.1.6); indeed, this appears to have happened in several fossil species (see SZALAY 1975). However, I believe that such events are side-issues as far as the evolution of the EPPRs is concerned. An explanation exists which is more likely than those considered above, and it is based on the ontogeny of the EPPRs found in modern strepsirhines.

It has been shown that the basic differences in the development of the EPPR in the two major strepsirhine groups are related to the degree of elaboration of sutural tissues at a critical stage in ontogeny combined with differing styles of petrosal pneumatization. The study of modern forms does not allow one to determine which of the two character states is the primitive one, but it does permit a reasonable model of the biological processes involved. As a minimal hypothesis, transitions in the EPPR could have arisen in the young stages of ancestral strepsirhines (1) through a gradual reduction in the degree of sutural tissue formation and an increased amount of pneumatic activity within the true tympanic cavity (assuming the transition was from the phaneric to the aphaneric condition); or (2) through the gradual acquisition of such tissues combined with decreased pneumatic activity within the true tympanic cavity (assuming the transition proceeded in the contrary direction).

This model suggests that the significant evolutionary changes would have occurred in young stages (fetal or early postnatal), no matter which direction the transition took. The corollary to this is that the change from one character state to the other may have been quite sudden when youthful innovations finally penetrated the adult stage through the action of neoteny or some similar process (see DE BEER 1958). While conditions in modern lorises and lemurs suggest that such an explanation for the appearance of the two character states might be very likely, there are great difficulties in proving this hypothesis due to the inadequacy of the strepsirhine fossil record in general and the complete absence of subadult ancestral lorises and lemurs in particular. Nonetheless, EPPR homologies between modern and ancestral strepsirhines are sufficiently great to indicate that this model is more parsimonious than others which have been suggested.

A final issue related to the construction of this model is whether alteration of the EPPR occurred only once during primate evolution, or whether such alterations have occurred several times.

SZALAY (1975), GINGERICH (1976) and CARTMILL (1975) have shown that several of the possible sequences for the course of primate evolution may actually demand that we interpolate a number of separate alterations into the record. Since I have not personally examined the relevant fossils and have not studied the ontogeny of the EPPR in non-strepsirhine primates, I cannot add anything substantive to their discussions. However, the existence of several fossil strepsirhines which are 'anomalous' for the EPPR (e.g., _Pronycticebus gaudryi_, _Progalago_ _dorae_, several of the subfossil Malagasy lemurs) indicates that the EPPRs were not unalterably fixed early in the evolution of the lorises and lemurs (see MACPHEE 1977). If there was lability in the relationship in early strepsirhines, then there is every reason to believe the EPPR could have repeatedly altered during the evolution of other primate lineages as well. Furthermore, it is not unlikely that sutural tissues played the operative role in these other change-overs as well. Some of these matters are discussed further in section 8.1.5.

3.1.6 OTHER TYMPANIC PROCESSES

The entoglenoid process of the squamosal overlaps the anterior surface of the bulla in the fashion seen in lemurs (see 2.1.8). There is no tympanic process of the alisphenoid.

Also lacking in strepsirhines is the broad basioccipital flange which overlaps the medial side of the petrosal plate in *Tarsius*.

3.2 DORSAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

The dorsal wall of lorises is quite similar to that of lemurs in most respects. An obvious difference is the smaller size of the roof, due to the different pattern of pneumatization and growth (see 3.3). The tegmen tympani is actually quite short relative to the size it attains in lemurs, but it nonetheless forms most of the roof of the tympanic cavity. The epitympanic wing of the petrosal is so small that it would not have been recognized as such were sectioned specimens not available.

There are also epitympanic wings of the sphenoid and squamosal, both of which appear in the dorsal wall.

3.2.1 TEGMEN TYMPANI, EPITYMPANIC WING OF THE PETROSAL, AND REICHERT'S CARTILAGE

3.2.1.1 Tegmen Tympani and Epitympanic Wing of the Petrosal

The tegmen tympani originates as usual from the anterolateral part of pars canalicularis and passes over most of the ossicular chain.

In *G. demidovii* MPIH 102 and MPIH 125 the tegmen is completely cartilaginous (fig. III-3). The sulcus for the facial nerve crosses the base of the tegmen on its way to the foramen stylomastoideum primitivum. The stapedial artery leaves the presumptive tympanic cavity through a very large foramen in the anterior part of the tegmen (fig. III-3). A wide gap, the piriform fenestra, separates the tegmen tympani from the promontory and the sphenoid.

In *G. demidovii* MPIH 120, the tegmen has grown a substantial amount and is extensively ossified. Posteriorly, the tegmen is now in bony continuity with the lateral surface of the promontory in the region of the foramen faciale. A fossa for the tensor tympani can also be detected at this stage, subdivided (as in lemurs) by the posterior part of the piriform fenestra. The stapedial artery travels across the tegmen in a deep sulcus (fig. III-1), but it is not enclosed within a canal. Its foramen of exit now lies in the middle of the tegmen rostralwards. The tegmen is nearly in contact with the large epitympanic wing of the sphenoid, and the anterior part of the piriform fenestra is mostly obliterated.

In the neonatal and postnatal specimens of *G. demidovii* and *G. senegalensis* the tympanic cavity is completely roofed over by bone.

The tegmen is entirely bony save for some areas along the petrosquamous suture. It is deeply excavated posteriorly by the developing epitympanic recess and its offshoot, the supracochlear cavity. Also in evidence is a minute epitympanic wing of the petrosal, formed by the petrosal plate where it extends from the anterior pole of the promontory.

In the adult Galago (fig. III-2), the tegmen forms most of the roof of the tympanic cavity. However, the rostralmost part is formed by the epitympanic wing of the petrosal and the exposed part of the epitympanic wing of the sphenoid (cf. lemurs, 2.2.1.1). It is not always possible to identify the foramen for the stapedial artery, but in cases in which it is distinct it lies just in advance of the epitympanic crest.

The tegmen has much the same structure in Loris and does not require separate description.

3.2.1.2 Reichert's Cartilage

Reichert's cartilage is similar in shape in all strepsirhines. However, it evidently ossifies somewhat later in Galago than in Microcebus, for the stylohyal center is not in evidence until after birth.

3.2.2 EPITYMPANIC WING OF THE SPHENOID

The epitympanic wing of the sphenoid is relatively larger in lorises than in lemurs, and as in the latter is almost entirely alisphenoidal in origin. Besides defining the superior wall of the tubal canal, the wing also participates in the roof of the tympanic cavity (figs. III-1, III-2).

3.2.3 EPITYMPANIC WING OF THE SQUAMOSAL

The ventral part of the squamosal is broader than in lemurs; otherwise, it participates in and bounds the same areas. It possesses a well-defined epitympanic wing which forms the lateral part of the roof of the tympanic cavity and the epitympanic recess.

3.3 PRINCIPAL SPACES AND SEPTA OF THE MIDDLE EAR

The following major pneumatic spaces of the middle ear form in lorises: the epitympanic recess, and the mastoid, supracochlear and medial accessory cavities. The hypotympanic sinus is so small that it may validly be regarded as absent.

The middle ear of lorises undergoes a pattern of pneumatization which is fundamentally different from the pattern found in lemurs. It is these contrasting patterns which are responsible for many of the structural differences in the auditory regions of adult strepsirhines. In lemurs, the hypotympanic sinus becomes the largest pneumatic space of the middle ear; the epitympanic recess is also well-developed, but the mastoid cavity is relatively small (except in a few species, such as Lepilemur mustelinus and Cheirogaleus trichotis), and the supracochlear cavity is almost non-existent. Lorises display the opposite pattern: the hypotympanic sinus is insignificant, while the mastoid and supracochlear cavities expand tremendously. Indeed, expansion of the latter two cavities and their communicating cellules is so extensive that they eventually surround the greater part of the auditory capsule, nearly isolating it from the cortical bone of the temporal. Although this difference in the pattern of pneumatization was recognized long ago by VAN KAMPEN (1905), the lack of sufficiently detailed ontogenetic descriptions has led many authors into mistaken views on the homologies of certain spaces and septa.

3.3.1 PRINCIPAL SPACES

3.3.1.1 Epitympanic Recess and Supracochlear Cavity

The true epitympanic recess, which contains the incudomalleolar joint, does not differ substantially from that of lemurs in its development or relations. In young postnatal specimens and in the adult loris, it is bounded by the epitympanic crest anteriorly, the facial canal medially, and the ampullar end of the lateral semicircular canal posteriorly.

The most important excavation, in terms of its end effects on otic anatomy, is the supracochlear cavity. The latter cavity arises as a medial evagination of the epitympanic recess into the dorsal surface of pars cochlearis. In G. demidovii MPIH 120, pneumatization has penetrated the bone roofing the foramen acusticum superius (for the vestibular branch of the VIII nerve). The growing space continues anteromedially in the dorsal surface of the petrosal and reaches the level of the fossa for the tensor tympani by the newborn stage. In the young infant (MPIH 1967/117), the cavity has inflated the arcuate eminence into a large hollow chamber and extends into the apex of the petrosal and the anterior part of the petrosal plate (fig. III-26). In later development, pneumatization proceeding from the supracochlear cavity continues to attack the petrosal plate, and eventually produces the anterior portion of the definitive medial accessory cavity (see 3.3.1.3).

3.3.1.2 Mastoid Cavity

In *Galago demidovii* MPIH 120, pneumatic activity in the rear of the epitympanic recess has excavated the base of the tegmen tympani and the adjacent wall of the pars canalicularis (fig. III-16). In later specimens this excavation leads to the aditus ad antrum and the antral cavity. In the neonatal specimens of *Galago* and in the near-term fetus of *Loris* the antrum has expanded into the cortical bone of the side-wall of the auditory capsule between the superior and lateral semicircular canals (figs. III-24, III-25). In the infant specimen of *Galago senegalensis* MPIH 1967/117 (fig. III-28), the mastoid cavity is quite large and displays some septal divisions. It is still actively expanding judging from the appearance of the bone and the amount of osteoblastic and osteoclastic activity (fig. III-28). Large segments of the semicircular canals are exposed within the cavity at this stage. Excavation has also extended ventrally into the posterior part of the petrosal plate (fig. III-28). Although the degree of inflation is still slight, one can visualize how the caudal section of the bulla is split into inner and outer lamellae as described by VAN KAMPEN (1905). The squamosal is also well pneumatized at this stage.

SABAN (1963) subdivides the mastoid cavity of the adult into the antrum proper and a large diverticulum D_4. He locates the antrum in the region of the posttympanic process, while the large ventral space seen in fig. III-2 behind the posterior wall of D_3 is separately identified by him as D_4. This usage is convenient, for D_4 is the pneumatic space which invades the posterior wall of the bulla and it is unrepresented in lemurs. It should be emphasized that D_4 is an extension of the mastoid antrum and not an independent excavation.

Fig. III-2 illustrates the position, extent and relations of the mastoid cavity (antrum, D_4, and associated cellules) in an adult Galago senegalensis. RAMASWAMI (1957:60, fig. 33) figures the mastoid cavity of an adult Loris tardigradus; in this genus the cavity as a whole is relatively smaller than in Galago and is not as extensively subdivided by incomplete septae and cellules (see also SABAN 1963, 1964).

3.3.1.3 Medial Accessory Cavity

It has already been noted that the medial accessory cavity is formed by the penetration of the mastoid and supracochlear cavities into the bone of the petrosal plate (fig. III-2). The formation of this cavity does not begin until after birth in Galago. In the ten-day old infant, MPIH 1967/117, both the supracochlear and mastoid (D_4) cavities have commenced their invasion of the bone of the petrosal plate (figs. III-26, III-33). In later ontogeny, these two cavities continue to advance towards each other and, as a consequence, to delaminate the petrosal plate into medial and lateral lamellae. In Galago, the two cavities usually meet under the promontory and so produce the definitive, complete medial accessory cavity (fig. III-2). In *Loris*, the splitting of the plate is usually not completed and the extensions of the mastoid and supracochlear cavities are separated by a thickness of bone in the adult. In this case, anterior and posterior medial accessory cavities may be distinguished. However, even in *Loris* there tends to be a connexion between the mastoid and supracochlear areas of inflation in the dorsal (cerebral) surface of the auditory capsule.

3.3.1.4 Hypotympanic Sinus

Despite the misleading appearance of the undissected adult lorisiform bulla, the hypotympanic sinus *sensu stricto* is so small that it cannot be usefully distinguished from the tympanic cavity proper. The reason for this is that virtually no pneumatic activity occurs in the ventral part of the tympanic cavity after birth. The moderately swollen appearance of the adult bulla is almost entirely due to the marked expansion of the medial accessory cavity within the petrosal plate.

It should be noted that SABAN (1963) regards the medial accessory cavity as part of the hypotympanic sinus (specifically, as the equivalent of diverticulum D_2 of lemurs). I do not find this to be a useful approach, since the medial accessory cavity is formed by the inflation of the mastoid and supracochlear cavities rather than by the outpouching of the tympanic cavity proper. It seems better to classify accessory pneumatic spaces according to their proximate origins, for this permits consistent usage in all cases.

The ontogenetic evidence is completely against a homology of the medial accessory cavity and SABAN's diverticulum D_2 of lemurs, for the former excavation is not represented in any known member of Lemuriformes.

There are shallow indentations of the anterior bullar wall on either side of the true anterior septum (see 3.3.2.1); these might be regarded as the equivalents of the rostral parts of D_1 and D_2 of lemurs (see fig. III-2). However, the degree of their inflation is negligible. For example, the D_2 of lorises does not even pneumatize the anteromedial process (which is excavated by the medial accessory cavity instead).

Diverticulum D_3 occupies the usual position behind the apertura fossulae fenestrae cochleae. It is properly regarded as part of the tympanic cavity per se (see 2.3.1.1).

3.3.2 PRINCIPAL SEPTA

3.3.2.1 Anterior Septum

A long-standing confusion exists concerning the true equivalent of the 'incomplete' anterior septum of lemurs (see 2.3.2.1). The anterior septum of lemurs is formed by the everted margins of the tegmen tympani and the epitympanic wing of the petrosal where they abut one another along the remnant portion of the piriform fenestra. However, almost every student of the strepsirhine auditory region has regarded the lateral lamina of the original petrosal plate (='complete' longitudinal septum of SABAN 1963 and many other authors) as the homologue of the lemuriform anterior septum. As we have seen (cf. 3.1.3.2, 3.3.1.3), the lateral lamina is produced by the splitting of the petrosal plate by the expansion of the mastoid and supracochlear cavities, a phenomenon which does not occur in lemurs.

In point of fact, the ontogenetic equivalent of the anterior septum is occasionally found in lorises. The last part of the piriform fenestra to close lies between the short epitympanic wing of the petrosal and the tegmen tympani, just as in lemurs (fig. III-2). The margins of these petrosal processes are usually flat, although I have found an actual ridge in some adult specimens of *G. senegalensis*. The ridge never attains large size, however, which may explain why it has been consistently overlooked. As in lemurs, the promontorial artery and various nerves pass through small foramina in the ridge.

3.3.2.2 Posterior Septum

SABAN (1963:272) states that the posterior septum is the bony wall separating the tympanic cavity from the petromastoid region; he also includes the incomplete septum carrying the carotid canal through the medial accessory cavity as part of the posterior septum (fig. III-2). The posterior septum of lemurs is apparently produced through the splitting of the posterior portion of the petrosal plate by the hypotympanic sinus (D_2); the posterior septum of lorises is also produced by pneumatic invasion, but the area from which pneumatization proceeds is the mastoid cavity (D_4). The question is then whether the two septa can be considered homologous. Much depends on the weight given to the method of pneumatization, and it is probably not useful to be too rigorous here. Perhaps the best course is to recognize the septa as partial homologues, since they form in the same area

Table 3-3

PRINCIPAL SEPTA OF THE MIDDLE EAR
(LORISIFORMES)

Terms Employed by SABAN (1963)	Terms Employed in this Study	Origin and Position
[not recognized]	anterior septum	petrosal (inconstant); forms on margins of tegmen tympani and epitympanic wing of petrosal along remnant portion of piriform fenestra (or its site, if obliterated) parasagittally, from anterior pole of promontory to tubal canal (covers promontorial a.)
septum principal (longitudinal)	[lateral lamella of petrosal plate]	petrosal; formed as a result of the pneumatization of the petrosal plate by the supracochlear and mastoid cavities parasigittally, from tubal canal to region of apertura fossulae fenestrae cochleae (where it continues laterally as septum between D_3 and mastoid cavity [latter septum derived from CTPP])
[not recognized]	epitympanic crest	petrosal; on tegmen tympani runs along anterior limit of epitympanic recess (crossed by stapedial a.)
septum transversal	[carotid canal and septum between mastoid cavity and D_3]	petrosal; formed as a result of the pneumatization of the petrosal plate (caudal part) carotid canal lies within medial accessory cavity

from the same material (posterior part of the petrosal plate), but are produced by different pneumatic 'fronts'.

There is no precise equivalent in lorises to the cave-like formation of the petrosal plate found in lemurs, the area in which pneumatization begins (see 2.3.2.2). The small diverticulum which is hollowed out of the medial section of the CTPP in galagines may perhaps be compared to the cave-like formation, since both have a close relationship with the internal carotid (figs. II-36, III-22). However, this diverticulum is absent in the near-term fetus of Loris (fig. III-33), and since it remains small throughout ontogeny it is difficult to homologize it with the entire posterior septum of lemurs.

A final complicating factor is the location of the posterior carotid foramen and canal; in lorises these structures lie medially, while in lemurs they are situated posteriorly or posterolaterally. There are good developmental reasons for this difference, however, and they will be explored under the appropriate heading (see 3.4.2).

3.3.2.3 Other Septa

As is well known, the mastoid cavity of some species of lorises is filled with a number of tiny ridges and septa produced during the excavation of the pars canalicularis and squamosal. There is also a well-marked epitympanic crest, which conducts the stapedial artery to its foramen of exit as in lemurs. There is no equivalent of the medial accessory septum of lemurs within the tympanic cavity proper, since the latter does not inflate onto the medial side of the promontory (see fig. III-2).

Small buttresses can also be found around the rim of the crista tympanica, on the intratympanic surface of the petrosal plate.

3.4 MUSCLES, ARTERIES AND NERVES OF THE MIDDLE EAR

3.4.1 OSSICULAR MUSCLES

The fibers of the tensor tympani arise from the shallow fossa situated along the juncture of the tegmen tympani and promontory in all specimens. The muscle inserts by means of a single tendon into the processus muscularis of the malleus and is innervated by the tensor tympani nerve, as usual.

I cannot confirm SABAN's (1963:270-271) observation that a second portion of the tensor tympani exists in lorises. This second portion, consisting of one or two slender fasicules, is said to pass from the Glaserian fissure to the head of the malleus in company with the anterior ligament. However, these slips are absent in the sectioned specimens of both Galago and Loris (cf. similar discordance in observations concerning the tensor tympani of Tupaia, section 4.4.1).

The stapedius muscle does not differ from that of lemurs. Its origin is entirely intratympanic (fig. III-24). The muscle is innervated by the stapedius nerve.

There is no element of Paaw.

2

3.4.2 ARTERIES

3.4.2.1 Introduction

The cephalic arterial pattern of lorises is illustrated in figs. II-41 and III-1.

The fact that the pattern of carotid circulation in Lorisiformes is very similar to that of cheirogaleid lemurs has often been noted (among recent papers, see SABAN 1963; SZALAY and KATZ 1973; CARTMILL 1975). As in these lemurs, the internal carotid and its promontorial and stapedial branches are extremely slender vessels which may partly obliterate during ontogeny. The circulus arteriosus is supplied by the vertebral-basilar system and by a vessel which closely resembles the anterior carotid of cheirogaleids. The latter will be referred to as such here.

The ontogeny and adult conditions of the carotid system of lorises are now known in fine detail, thanks to the studies of ADAMS (1957), SABAN (1963), KANAGASUNTHERAM and KRISHNAMURTI (1965), KRISHNAMURTI (1968), and BUGGE (1974).

3.4.2.2 Stem and Major Tympanic Branches of the Internal Carotid and Anterior Carotid Arteries in Lorises

The internal carotid is given off at the same time as the anterior carotid, or it may arise from the root of the latter vessel in some cases. It is always small, being about one-fifth to one-tenth the size of the anterior carotid in the sectioned specimens of Galago and Loris. It is said to be obliterated (or, at least, unidentifiable) in adults of Galago senegalensis and Nycticebus coucang by KANAGUSUNTHERAM and KRISHNAMURTI (1965), although this observation may be due to a processing artefact (injection masses do not always penetrate fine vessels).

After being released by the common carotid, the vessel enters the posterior part of the tympanic cavity from the medial and travels over the posterior pole of the promontory before dividing into promontorial and stapedial branches.

The promontorial and stapedial branches are present in all sectioned specimens, although in most of them the lumen of the promontorial artery in particular was constricted along the greater part of its length. It is obvious that the promontorial artery can supply little blood to the circulus arteriosus even if its lumen remains patent into adult life. The route of the promontorial artery is like that of Microcebus in most respects. In the younger sectioned specimens, in which the dorsal wall of the tympanic cavity is still incomplete, the artery traverses the lateral wall of the promontory and then freely passes over the anterior pole to join the cerebral carotid (i.e., the apparent continuation of the anterior carotid from the extracranial carotid rete; figs. III-13, III-21). In the older specimens and in the adult, the promontorial artery passes between the epitympanic wings of the sphenoid and petrosal, above the tympanic aperture of the tubal canal and thence to the cerebral carotid while the latter is still in the anterior carotid foramen. The promontorial artery does not send a branch to the pterygoid canal.

The stapedial artery retained its connexion with the internal carotid in all sectioned specimens, although its proximal segment can undergo the same degenerative changes seen in the promontorial artery (KANAGASUNTHERAM and KRISHNAMURTI 1975). Its distal segment (i.e., the medial meningeal) remains open because it is supplied by an anastomotic branch from the circulus arteriosus (BUGGE 1974).

The stapedial artery is given off at a more anterior level than in Microcebus (fig. III-1). Consequently, it must travel backwards as well as upwards in order to pass through the obturator foramen of the stapes. After passing through the latter it crosses the path of the facial nerve (fig. III-14), and then leaves the tympanic cavity through a foramen in the tegmen tympani. In the specimens of Galago demidovii the artery is accommodated in a deep groove from the facial sulcus to the foramen in the tegmen; in the specimens of Galago senegalensis, the groove has been converted into a canal (fig. VII-6). In the adult, a foramen adjacent to the epitympanic crest can sometimes be recognized (fig. III-2); this aperture is evidently for the stapedial artery. The stapedial does not release any branches within the tympanic cavity in the sectioned specimens. Accordingly, the ramus mandibularis and infraorbitalis are fed by the internal maxillary of the external carotid (BUGGE 1974).

The anterior carotid is the equal of the external carotid in calibre (or it may be even slightly larger), but it is quite short. Its route and connexions are very similar to those of Microcebus, and the homology of the anterior carotids in these strepsirhines can scarcely be questioned (see CARTMILL 1975). The single major difference between the two is the presence of the simple extracranial rete at the distal end of the anterior carotid, presently known only in lorises.

KANAGASUNTHERAM and KRISHNAMURTI (1965) have described the embryogeny of the rete in young specimens of _G_. _senegalensis_. It develops independently of the promontorial artery, although the latter eventually forms a connexion with it. It is described as 'simple' for the reason that it generally consists of several large interlacing branches rather than a complex network of much finer vessels (as in the intracranial carotid rete found in ungulates and certain other mammals; see DANIEL, DAWES and PRITCHARD 1953).

It should be noted that the number of branches involved in the rete is quite variable within the different lorisoid genera (although galagines, on the whole, display a greater degree of retial development than do lorisines; see BUGGE 1974). _Galago senegalensis_ and _Nycticebus coucang_ represent opposite extremes; in the former, there may be up to eight major channels in the rete (DU BOULAY and VERITY 1973; this study), while in the latter the rete _per se_ may be absent (SABAN 1963). However, individual variability also exists. In _Nycticebus coucang_, for example, retia of single specimens may be as extensive as those of other lorisines (see KANAGASUNTHERAM and KRISHNAMURTI 1965).

The function of the extracranial carotid rete is still obscure. ASK-UPMARK (1953) suggested that it protects the brain from large arterial pulses in the anterior carotid, since this vessel is not enclosed within a bony canal as is the true internal carotid (or promontorial artery). KRISHNAMURTI (1968) argues that pulsations of the anterior carotid and the rete may assist venous return from the cavernous sinus to the petro-occipital sinus. The basis for this argument is the observation that a venous lake, consisting of a number of channels, surrounds the branches of the carotid rete. Replacement of one thick-walled artery by a number of thinner-walled interlacing branches would enhance arterial expansion and thus press upon the valveless channels of the venous lake. Note that this explanation demands increased arterial metering through the carotid rete, which is the reverse of ASK-UPMARK's (1953) view.

CARTMILL (1975) dismisses both of these explanations in favor of a thermoregulatory argument: venous blood draining from the cavernous sinus to the venous lake surrounding the carotid rete cools the arterial blood passing through the anterior carotid to the circulus arteriosus. The evidence for this physiological mechanism is based on the experimental findings of BAKER and HAYWARD (1967, 1968; see also BAKER 1972) for certain ungulates and carnivores possessing intracranial retia on branches of the external carotid. The function of the retia in these mammals may be directly linked to the maintenance of brain temperature. However, no data exist for strepsirhines regarding possible differentials between cerebral arterial blood and aortic temperature, and despite CARTMILL's compelling application of the thermoregulatory argument it is still moot whether or not a cooling function can be attributed to the lorisiform rete and associated venous plexus.

In this context, it is curious that retia do not exist in any known cheirogaleid, since the function of the anterior carotid is presumably the same. CARTMILL suggests that retial formation may be size-dependent, with larger forms possessing more complicated arterial nets than smaller ones. On this basis he also speculates that retia may yet be found in larger cheirogaleids, such as Phaner. Existing data on retial complexity in species of Galago, although admittedly poor, does not precisely conform to CARTMILL's expectations. According to DU BOULAY and VERITY (1973), it is the intermediate-sized species, G. senegalensis, which has the highest development of the carotid rete (up to eight major branches). The smaller species, G. demidovii and G. alleni, have three and five branches respectively, while the largest, G. crassicaudatus, has only four.

A somewhat analagous difference in retial development exists in carnivores. Arterial nets are found on branches of the external carotid in a number of carnivore families, but not in ursids or the giant panda, Ailuropoda. However, in the latter the medial carotid (which is not the homologue of the anterior carotid) is very well-developed and follows a looping, tortuous course around either the cavernous or inferior petrosal sinuses. HUNT (1974) argues that the complicated course of the medial carotid around venous channels in bears may serve to cool arterial blood headed for the brain, as do the retia of other carnivores. One might expect to find a similar situation in cheirogaleids (if indeed the thermoregulatory function exists in dwarf lemurs), but this is apparently not the case. Although there is a close association between the petro-occipital sinus and the anterior carotid in cheirogaleids, the artery follows a straight course to the cavernous sinus.

3.4.2.3 Foramina

(1) Anterior Carotid Foramen

The cerebral carotid is formed by the union of the anterior carotid (distal to its rete) and the promontorial artery, and it is this joint vessel which passes through the anterior carotid foramen along with the petro-occipital sinus.

A complete foramen caroticum primitivum is not formed in lorises because of the absence of the alicochlear commissure (HENCKEL 1928; RAMASWAMI 1957; this study). Otherwise, foraminal development is identical to that found in cheirogaleid lemurs (see 2.4.2.4). As in the latter, the definitive anterior carotid foramen of the adult loris is visible on the ventral surface of the skull between the sphenoid and the anteromedial process of the bulla.

(2) Posterior Carotid Foramen

In section 2.4.2.4, it was noted that the entry-point of the internal carotid into the tympanic cavity shifts during ontogeny in lemurs, from an originally medial position to one which is more posterior or posterolateral. The agencies responsible for this shift were identified as (1) the growing petrosal plate, which considerably depresses the artery before finally growing around it; and (2) the pneumatization of the original CTPP, which increases the breadth of the posterior wall of the bulla and causes a further (apparent) shift in the position of the posterior carotid foramen.

In lorises, developmental conditions are quite different. Neither bullar growth nor pneumatization have any marked influence on the entry-point of the internal carotid, which remains positionally the same throughout ontogeny. The essential reason for this is that the petrosal plate entraps the artery during the earliest phases of the former's development (fig. III-1). Enclosure binds the artery to the medial wall of the apertura fossulae fenestrae cochleae, where it cannot be affected by the ventral growth or later pneumatization of the petrosal plate.

The posterior carotid foramen itself is only slightly modified during bullar development. The original, large foramen becomes subdivided by bony partitions into a number of apertures for the separate vessels and nerves which pass through it. Also, pneumatization of the petrosal plate results in the creation of bony canals for these same vessels and nerves within the confines of the medial accessory cavity (fig. III-2).

3.4.3 NERVES

The major nerves traversing the tympanic cavity in Galago are illustrated in fig. III-1. There are few significant differences from Microcebus and extensive description is not required here.

In the fetus, the auricular ramus of the vagus and tympanic nerve share a common foramen with the internal carotid artery and nerve. In Galago, this foramen becomes subdivided in later ontogeny into several small apertures (mastoid and tympanic canaliculi and posterior carotid foramen). In Nycticebus, the tympanic nerve and internal carotid artery (and nerve) may share the same foramen according to SABAN (1963).

In the adult loris, bony canals conduct these nerves through the medial accessory cavity (fig. III-2).

There is no element of Spence associated with the chorda tympani.

3.5 SUMMARY OF PRINCIPAL FINDINGS

(1) The fibrous membrane of the tympanic cavity forms the ventral wall of the presumptive middle ear cavity prior to the appearance of the tympanic processes of the petrosal, which functionally replace it.

(2) The bony ventral wall is formed by the petrosal and the ectotympanic. As in lemurs (see 2.5), both the RTPP and CTPP are formed, and they join together to produce the petrosal plate. The plate later fuses with the rim of the ectotympanic (shortly after birth) to form the compound bulla characteristic of lorises. The CTPP ossifies as in lemurs.

(3) Secondary cartilage was not identified in the petrosal plate of fetal lorises available for study. There is no evidence of an entotympanic element.

(4) The ectotympanic becomes more or less expanded to the lateral in the different species of lorises, but it nonetheless retains the bony architecture of fetal life ('intermediate bone'). It is still possible to separate the material of the petrosal plate

from that of the (original) ectotympanic in sectioned adults.

(5) Lorises retain the edge-to-edge articulation of the petrosal plate and ectotympanic throughout life. It is suggested that this happens because a complete array of sutural tissues are elaborated at the ectotympanic-petrosal plate interface early in bullar ontogeny, and because the effects of pneumatization within the tympanic cavity proper are negligible. Accordingly, nothing disturbs the original condition of the ectotympanic-petrosal plate relationship. It is not suggested that edge-to-edge articulation of bone territories necessarily induces fusion, although it would appear to be a necessary precondition.

(6) As in lemurs, outgrowths of the sphenoid and entoglenoid region of the squamosal may slightly overlap the petrosal plate, but they are not found within the ventral wall _per se_.

(7) The tegmen tympani and the epitympanic wings of the petrosal, sphenoid and squamosal all contribute to the dorsal wall of the tympanic cavity. The contributions of the epitympanic wings of the petrosal and sphenoid are small but detectable.

(8) As in lemurs, the piriform fenestra is reduced to a narrow slit during ontogeny and may be entirely obliterated in the adult.

(9) Pneumatization has important effects on the bony walls of the middle ear, but it follows a different course than in lemurs. Specifically, pneumatic activity is concentrated in the dorsal and rear walls of the middle ear, rather than in the ventral wall. The

mastoid and epitympanic-supracochlear cavities expand enormously; they eventually invade the substance of the petrosal plate, splitting it into two lamellae. This creates a new cavity, the medial accessory, which is entirely unrepresented in lemurs. The hypotympanic sinus is small or absent, and the lateral lamella of the original petrosal plate occupies the position of the primordial plate on the ventral surface of the promontory. The homologies of the septa of the middle ear are discussed.

(10) Findings respecting the ossicular muscles and the branchings of the carotid are generally in agreement with those of other authors. The origin of the stapedius muscle is entirely intratympanic. The anterior carotid is probably the homologue of the ascending pharyngeal artery, as in cheirogaleid lemurs. The routes and connexions of the principal nerves passing through the middle ear are also discussed.

CHAPTER FOUR

TUPAIOIDEA

METHOD OF DESCRIPTION

4.1 VENTRAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

- 4.1.1 Fibrous Membrane of the Tympanic Cavity
- 4.1.2 Cartilage of the Auditory Tube
- 4.1.3 Entotympanic
- 4.1.4 Tympanic Processes of the Petrosal
- 4.1.5 Ectotympanic
- 4.1.6 Relationship of the Ectotympanic and Entotympanic
- 4.1.7 Linea Semicircularis
- 4.1.8 'Anulus Membrane'
- 4.1.9 Other Tympanic Processes

4.2 DORSAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

- 4.2.1 Tegmen Tympani, Epitympanic Wing of the Petrosal and Reichert's Cartilage
- 4.2.2 Epitympanic Wing of the Sphenoid
- 4.2.3 Epitympanic Wing of the Squamosal

4.3 PRINCIPAL SPACES AND SEPTA OF THE MIDDLE EAR

- 4.3.1 Principal Spaces
- 4.3.2 Principal Septa

4.4 MUSCLES, ARTERIES AND NERVES OF THE MIDDLE EAR

- 4.4.1 Ossicular Muscles
- 4.4.2 Arteries
- 4.4.3 Nerves

4.5 SUMMARY OF PRINCIPAL FINDINGS

4.1 VENTRAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

In Tupaiinae, the ventral wall is formed by a greatly-inflated entotympanic element (probably the rostral entotympanic) and a tiny caudal tympanic process of the petrosal (latter definitely known to exist only in *T. glis*; see fig. IV-5). In *Ptilocercus* there is, in addition, an extremely well-developed tympanic process of the alisphenoid.

Although the ectotympanic is intrabullar, as in lemurs, bullar overgrowth is achieved by different means.

There are no large rugosities on the entotympanic for muscle attachments, even in the larger species such as *Urogale everetti*.

4.1.1 FIBROUS MEMBRANE OF THE TYMPANIC CAVITY

4.1.1.1 Structure, Relations and Development

SPATZ (1966:29,32) noted that a connective-tissue membrane (the fibrous membrane of this study) ventrally encloses the tympanic cavity in young stages of *T. glis*.

The fibrous membrane is strikingly elaborated in MPIH 1960/82a and MPIH 1959/4 (figs. IV-7, IV-8); its degree of development exceeds that of any form described in this study, with the possible exception of the fetus of *Propithecus* sp. (fig. II-31). On the other hand, at the gross level, it does not appear to differ appreciably from the fibrous membranes found in young stages of strepsirhines and lipotyphlans, except perhaps for a denser concentration of collagen

Table 4-1

TUPAIOIDEA

SPECIMENS	No.	CRL[1]	HL[2]	ST[3]	PS[4]	STAIN
TUPAIINAE						
Tupaia glis						
I. Near-Term Fetus	MPIH 1960/82a	54	23	15	cross	Azan
II. Newborn	MPIH 1959/4	59	25	12	cross	Azan
III. 8 Days Postnatal	MPIH 1960/77	--	29	15	cross	Azan
IV. 19 Days Postnatal	MPIH 1964/10	--	--	15	cross	Azan
V. Adult	MPIH 1961/11	--	50	15	cross	Azan

[1] Crown-rump length (in mm)

[2] Head Length (in mm)

[3] Section thickness (in mμ)

[4] Plane of sectioning

NOTES ON SPECIMENS

The specimens listed above are the same as those described by SPATZ (1964, 1966) in his examination of general cranial development and bullar ontogeny in *Tupaia glis*.

In addition to this material, Prof. Dr. D. STARCK permitted me to study the models of MPIH 1959/4 (entire cranium) and MPIH 1964/10 (left auditory region) made by Dr. SPATZ, which are now in the collections of the Anatomisches Institut, J.-W.-Goethe Universität, Frankfurt/M.

Also available for study were macerated skulls of adult specimens of *Tupaia glis*, *T. javanica*, *T. minor*, *T. nicobarica*, *Dendrogale melanura*, *Urogale everetti*, *Lyonogale tana*, and *Ptilocercus lowii*, on loan to Dr. D.G. STEELE (Department of Anthropology, The University of Alberta, Edmonton) from the U.S. National Museum, Washington, D.C.

fibres. The membrane is slightly lamellated in some specimens.

The relations of the fibrous membrane to other structures of the basicranium are similar to those already described for lemurs and lorises, although there are some differences which are worthy of note (see 4.1.1.2).

The membrane is most easily studied in stages prior to those in which there is significant bullar development. As in the youngest strepsirhine fetuses, the membrane in MPIH 1960/82a (near-term fetus) separates the developing cavum tympani and tympanic mucoid tissue from adjacent tissues lying medially and ventrally to the auditory capsule (figs. IV-7, IV-19, IV-23). Anteriorly, the perichondrium of the anterior mass of cartilage (cartilage of the tube + entotympanic; see 4.1.3) is embedded within the fibrous membrane. Medially and posteriorly, the membrane is continuous with the dense connective tissues lining the central stem and the rear of the auditory capsule.

Like lipotyphlous insectivores, but unlike strepsirhines, the lateral section of the CTPP arises medial to the origin of the stapedius muscle (see fig. I-2). Further, the fibrous membrane attaches to this latter outgrowth rather than to the posterior continuation of the crista parotica (figs. IV-22, IV-23). Thus, the origin of the stapedius muscle is excluded from the presumptive tympanic cavity as defined by the membrane (cf. conditions in Microcebus murinus, 2.1.1 and fig. II-16; and Elephantulus fuscipes, 5.1.1).

The relationship of the fibrous membrane to the periosteum of the ectotympanic is extremely weak. In MPIH 1960/82a (fig. IV-7) the two are not even in contact. In the older specimens, there is a small ventral area where the two meet (figs. IV-12, IV-13, IV-14), but the degree of intimacy is much less than in lemurs (figs. II-9, II-12).

The fibrous membrane loses definition lateral to the position of the ectotympanic, although in some sections it appears to reach the perichondrium of the auricular cartilage. Reichert's cartilage, the internal carotid artery, and various nerves penetrate the membrane posteriorly (fig. IV-21).

4.1.1.2 Fibrous Membrane and the Entotympanic

There is a principal difference between tupaioids and strepsirhines in the relationship of the fibrous membrane to the bullar rudiment. In strepsirhines, the petrosal plate develops adjacent to the membrane (see 2.1.3 and 3.1.3); it originates as an excrescence of the petrosal bone and is always embedded in the latter's periosteum. In *T. glis*, however, the entotympanic develops *within* the fibrous membrane (figs. IV-12, IV-13, IV-14), and, of course, has no primary relationship with the petrosal (see 4.1.3). It is noteworthy that the entotympanics of *Elephantulus fuscipes* display similar relations (see 5.1.1).

4.1.2 CARTILAGE OF THE AUDITORY TUBE

It is not possible to define the precise extent of the cartilage of the tube in any of the sectioned specimens except the adult (MPIH 1961/11). The reason for this is that the entotympanic and the tubal cartilage appear to be fused from the very first, at least on present evidence (SPATZ 1966). The significance of this fusion will be discussed further in section 4.1.3.2. Here, it will be sufficient to describe conditions in the youngest specimen (MPIH 1960/82a), in which entotympanic material is probably already present, and to relate them to the anatomy of the rostral end of the auditory region as it appears in the adult (MPIH 1961/11). In this way it is possible to shed some light on where to draw the boundary between the entotympanic and the cartilage of the tube.

In the near-term fetus there is an anterior mass of cartilage which has all of the normal relations of a cartilage of the tube. Specifically, it is situated in the anteromedial part of the otic region and guides the auditory tube into the presumptive tympanic cavity (fig. IV-16, IV-17). The most conspicuous features of this anterior mass include its lengthy anteroposterior and mediolateral dimensions and structural complexity. Anteriorly, it consists of broad dorsal and medial plates. The medial plate extends posteriorly to the region of the anterior pole of the promontory (figs. IV-18, IV-19), while the dorsal plate comes to an end sooner in cross-sections. At this stage the anterior mass is entirely free of any connexions with other elements in the auditory region, but it has a close association with the fibrous membrane of the tympanic cavity (see 4.1.1).

Compared to the fetuses of other forms described in this study, the anterior mass of cartilage is exceptionally large. It might be expected that the anterior mass would occupy a proportionately large area in the adult if it were entirely tubal cartilage. However, in the sectioned adult (MPIH 1961/11), the only cartilaginous area remaining in the anterior end of the auditory region is very small and in direct association with the auditory tube (fig. IV-38a,b). This cartilaginous area must be identified as the cartilage of the auditory tube, but it extends no further posteriorly than the pharyngeal aperture of the tubal canal to which it attaches.

What, then, is the fate of the anterior mass of cartilage described for the near-term fetus (MPIH 1960/82a)? Most of it is replaced by bone, as later stages show,and only a small fraction becomes the (true) cartilage of the tube. While it is not possible to demarcate exactly the part of the anterior mass which is tubal cartilage in the sub-adult specimens, a convenient structural boundary is provided by the anterior septum. This septum (see 4.3.2) is ossified in the adult and is, of course, considered to be part of the entotympanic. Since it extends up to the anterior wall of the bulla (fig. IV-3), its place of origin there may be taken to be the rostralmost point of the entotympanic in young specimens. The most economical view would be to regard the cartilage in front of this point as tubal, as it is in direct association with the auditory tube, and the cartilage posterior to this point as entotympanic, for it is later entirely replaced by bone (figs. IV-1, IV-2, IV-16, IV-17). Unless some such structural division is made, one would have to argue for the endochondral replacement of true tubal cartilage--which is presumably an unlikely event. It may be mentioned that the approach taken here is different from that of SPATZ (1966), who did not attempt to define a structural boundary between the two in fetuses.

It remains to add a few details concerning the cartilage of the tube in the adult specimen. It is highly irregular in shape and is tightly bound to the anterior extremity of the entotympanic bone by dense connective tissue representing their conjoined periosteum/perichondrium. Significantly, there is no zone where cartilage grades into bone--or even isolated areas of calcified cartilage--in the region where the tubal cartilage adjoins the entotympanic (fig. IV-38a,b). This indicates that there must be some real boundary between the two elements in earlier stages of development, even if this boundary cannot be visualized histologically. Otherwise, the whole anterior mass should have ossified once the entotympanic ossific center appeared (see 4.1.3).

No accessory cartilages were present in any of the sectioned specimens.

4.1.3 ENTOTYMPANIC

4.1.3.1 Introduction

In the only thorough investigation of bullar ontogeny in tupaioids which has been undertaken, SPATZ (1966) placed beyond doubt

VAN KAMPEN's (1905) contention that the greater part of the auditory bulla develops from a separate endochondral ossification which must be regarded as an entotympanic. Historically, there had been some confusion regarding the origin and significance of this element in tree shrews. The earliest interpretation (e.g., LECHE 1885; WINGE 1892 [1941]) was that the bulla was an expanded ectotympanic (as in rodents, for example). The free anulus bordering the tympanic cavity was thought to be a secondarily-detached part of the ectotympanic which had in some fasion gained its independence. This view, which requires the splitting of the ectotympanic into two elements, is extremely unlikely. VAN KAMPEN (1905) found that the bulla was completely separate from all other bones of the auditory region, including the petrosal, in a young specimen of Tupaia (but see 4.1.4). On this basis he concluded that the bulla must be formed from an entotympanic. Although often cited as the authority for the entotympanic origin of the tupaioid bulla, it may be noted that VAN KAMPEN lacked the appropriate young specimens for the unequivocal demonstration of the independence of the entotympanic element, as he himself conceded (1905:448).

In the ensuing years, the ontogenetic independence of the entotympanic became generally accepted, but its evolutionary significance was clouded when the debate regarding tupaioid-primate affinities was kindled. LE GROS CLARK (1959), for example, suggested that the entotympanic of tree shrews was simply a portion of the petrosal which had acquired developmental independence. This theory (which is not the most likely possibility by any means) tended to reduce the significance of the difference in bullar construction between tupaioids and primates to one of degree rather than kind, and was prominent in LE GROS CLARK's (e.g., 1925, 1934, 1959) advocacy of tupaioid membership in the primates.

Still later, the situation became confused anew with SABAN's (1956-57) claim that there was no suture between the petromastoid region and the bulla, although there was one elsewhere which separated the latter and the promontory. Although SABAN studied only adult specimens, he concluded from his observations that the bulla must be an outgrowth of the petromastoid, and that a separate entotympanic was absent. In fact, SABAN's assertion that a suture is absent between the petromastoid and the bulla in adult tree shrews is substantially correct, but not because the bulla is an outgrowth of the petromastoid. SPATZ (1966) established that a small CTPP forms in _Tupaia_ (and presumably in other tupaioids), and that this process fuses with the posterior end of the entotympanic while both are still cartilaginous. Evidently, no suture remains between the two when they later ossify (see 4.1.4). SABAN's understandable error underscores VAN DER KLAAUW's (1930) caveat that determinations of the construction of adult auditory bullae must always be made with great care because of the possibility of the ontogenetic obliteration of boundaries between separate elements.

SPATZ (1966) has already described the development of the entotympanic in the sequence of specimens used for this study. His fine report requires few additions, but for the sake of completeness and later comparisons with other forms, his major findings and a few additional observations will be presented here.

4.1.3.2 Structure, Relations and Development of the Entotympanic

One of the great difficulties which has complicated both the ontogenetic and phylogenetic analysis of the mammalian entotympanic is its pronounced tendency to form intimate associations with a variety of other structures in the auditory region.

In the case of *Tupaia*, early associations are formed with the cartilage of the tube, CTPP and tegmen tympani. The connextion formed with the cartilage of the tube is the most troublesome to evaluate because on present evidence it appears to exist *ab initio*. SPATZ (1966) was unable to separate sharply the material of the cartilage of the tube from that of the entotympanic, as there is no histological and only an indefinite structural boundary between the two in the young stages he investigated. However, primary fusions of the entotympanic with the cartilage of the tube have been observed in other mammals (VAN DER KLAAUW 1929, 1931; REINBACH 1952), and it remains possible that the initial independence of the entotympanic might be demonstrable in a larger series of late-fetal specimens. In any case, it would be quite premature to conclude that the tupaioid bulla is formed from an hypertrophied tubal cartilage *per se*.

It was suggested (see 4.1.2) that a convenient structural boundary can be drawn between the two elements composing the anterior mass of cartilage in young specimens by reference to conditions in the adult. In young specimens, it is at least reasonable to regard as true tubal cartilage the relatively small amount of cartilage anterior to the nascent anterior septum, and as entotympanic cartilage everything posterior to the rostral extremity of that structure. Accordingly, most of the medial plate and a large portion of the dorsal plate of the anterior mass must be regarded as entotympanic, and will be described as such here (see figs. IV-1, IV-2).

The associations with the tegmen tympani and CTPP are secondary and are formed while all structures involved are still cartilaginous. A partial suture eventually appears at the site of the entotympanic-tegminal commissure, and the two are easily separated in the adult skull. This is not the case with the entotympanic-CTPP association: the two structures completely fuse and are inseparable in the adult. Unlike some other mammals in which the development of the entotympanic(s) have been studied, there is no primary association with Reichert's cartilage (figs. IV-35, IV-41).

Tupaia glis MPIH 1960/82a
(near-term fetus)

In the earliest stage investigated by SPATZ (1966), an anterior mass of cartilage of uniform composition is the only independent chondrified element in the ventral wall of the tympanic cavity. The structure of this anterior mass and its provisional subdivisions have already been described (see 4.1.2).

The caudally-directed medial plate is firmly appressed to the fibrous membrane of the tympanic cavity, and its posterior apex actually terminates within this membrane (figs. IV-18, IV-19).

Tupaia glis MPIH 1959/4
(newborn)

In the neonate, a long cartilaginous spur extends from the previously-described medial plate of the anterior mass to the level of the presumptive posterior carotid foramen (figs. IV-1, IV-25, IV-26). Although the caudal spur is clearly in younger cartilage than the rest of the anterior mass, once again an histologically-sharp boundary is absent. Even if the subdivision of the anterior mass into tubal and entotympanic material must remain in doubt, the caudal spur has to be regarded as entotympanic because of its position in the ventral wall and its later fate.

SPATZ' (1966) impression is that the spur is a caudal outgrowth of the medial plate, rather than a separate element which has fused to the anterior mass. Since the evidence for the subdivisions employed here is inconclusive at best, nothing can be said about the possibility that both a rostral and a caudal entotympanic may be present in Tupaia. Since the entotympanic grows posteriorly from the region of the cartilage of the tube, the simplest conclusion is that only a large rostral entotympanic is present (see VAN VALEN 1965:146; and 4.1.3.3).

An important observation for later discussion is the relation of the caudal spur to the fibrous membrane of the tympanic cavity. The spur lies completely within, rather than simply against, the fibrous membrane (fig. IV-12). The significance of this is that there is a certain amount of evidence (see 5.1.4 and 8.5.2) which suggests that the fibrous membrane actively gives rise to entotympanic material. The development of the tupaioid entotympanic would thus stand in marked contrast to that of the strepsirhine petrosal plate (in the histogenesis of which the fibrous membrane apparently plays no role).

Fig. IV-12 illustrates one of the bases for this conclusion. The fibrous membrane not only completely encases the entotympanic cartilage, but also appears to function as its perichondrium. This is most evident towards its medial and lateral margins. The central part is in young cartilage, individual chondrocytes being separated by only a small amount of hyaline matrix (cf. the much older cartilage composing the promontory in the same figure). This young cartilage grades, on either side, into densely-aggregated cells of precartilage and finally into the fascia-like material of the fibrous membrane.

The anterior septum is now well-defined (fig. IV-24) and is ventrally in close association with the anterior crus of the ectotympanic. The dorsal plate (also considered to be mostly entotympanic in origin) is slightly larger than in the previous specimen and is also in close relation with the ectotympanic.

Tupaia glis MPIH 1960/77
(8 days old)

The entotympanic has grown considerably in size mediolaterally and now hides a large portion of the promontory and the medial part of the ectotympanic crura (fig. IV-2).

The secondary associations with the CTPP and tegmen tympani are completed during this stage. In both cases of synchondrosis, the site of fusion can be easily identified because of histological differences between the cartilaginous structures involved (figs. IV-29, IV-30, IV-31).

The cartilage composing the entotympanic is clearly older than in MPIH 1959/4(newborn). The hyalin matrix is highly elaborated in the central portions of the entotympanic, but as yet there is no sign of an ossification center (fig. IV-13).

As in the neonate, the posterior part of the entotympanic is completely embedded within the fibrous membrane of the tympanic cavity. In cross-sections through the middle of the entotympanic (fig. IV-13), there is a continuous gradation in cell and matrix type, from mature chondrocytes in prominent lacunae in the center to spindle-shaped fibroblasts in a thick fibrous matrix at the peripheries. Another feature which suggests the direct production of cartilage from the fibrous membrane is the form of the entotympanic: it is broad but thin. One might expect it to be substantially thicker if growth were mainly interstitial rather than appositional.

Tupaia glis MPIH 1964/10
(19 days old)

In this postnatal specimen the bulla is beginning to approach adult morphology in several respects. The ectotympanic is almost entirely concealed by the bulla by this stage (fig. IV-34), and only a relatively thin strip of the petrosal is left exposed between the entotympanic and the basioccipital (fig. IV-35). Further, whereas in previous stages the entotympanic was entirely cartilaginous, it is now undergoing ossification.

Anteriorly, ossification extends throughout the anterior septum and most of the anterior wall of the bulla (fig. IV-33, IV-34). Only the most rostral section of the original anterior mass of cartilage is completely unmineralized (fig. IV-32). This section, or part of it, is believed to give rise eventually to the true tubal cartilage (see 4.1.2). The superior part of the entotympanic, which forms part of the roof of the middle ear, is also substantially bony (fig. IV-34).

The area of fusion with the anterior end of the tegmen tympani is still cartilaginous, even though the tegmen itself is substantially bony posterior to the entotympanic-tegminal commissure. This supports SPATZ' (1966) contention that the entotympanic probably ossifies from its own center rather than from the tegmen tympani. Close inspection of serial sections indicates that the center of ossification first appears in the superior part of the entotympanic, in the region of the anterior septum (fig. IV-34).

Posterior to the level of the anterior septum the degree of ossification and mineralization decreases; most of the original caudal spur is still in cartilage (fig. IV-35).

The CTPP is entirely bony, and in some areas trabeculae seem to extend from this process into the actual substance of the entotympanic; calcified cartilage is present within the entotympanic in such areas (fig. IV-36). In other areas, however, the CTPP and entotympanic are clearly separated from one another by an amorphous zone of fibers (fig. IV-37). The peculiar conditions in this region of the entotympanic may explain why no entotympanic-CTPP suture appears in the adult. Note (fig. IV-35) that the entotympanic and Reichert's cartilage are now in close contact, but are not fused.

The entotympanic is joined to the promontory only by means of a thin layer of connective tissue, and the promontory obviously takes no part in the ossification of the entotympanic.

SPATZ (1966) constructed a model of the left auditory region of this specimen, but did not illustrate and only briefly described it. Interestingly, the general aspect of the model resembles the bulla of adult Ptilocercus more strongly than that of adult Tupaia. Some of the features which produce this impression are due to differences in inflation and bony development between the two genera (LE GROS CLARK 1926). For example, in Ptilocercus the entotympanic does not cover as much of the medial side of the promontory because the hypotympanic sinus inflates less. In MPIH 1964/10, bullar inflation is only barely under way and a large medial strip of the petrosal is still exposed (fig. IV-10, IV-35). Another feature which indicates that the ptilocercine bulla is less developed than that of Tupaia is the condition of the external auditory meatus. In adult Tupaiinae, the meatus is slightly drawn outwards into a small external acoustic canal (fig. IV-5), whereas in Ptilocercus there is no suggestion of a canal whatsoever (fig. IV-42). Moreover, the aperture of the meatus is relatively larger than in Tupaiinae. Correlated with this difference is the fact that the lateralmost part of the external auditory meatus is the last to form during bullar ontogeny. In the model of the nineteen-day old specimen, the entotympanic has not completed its development, and the aperture of the meatus is consequently large and without the semitubular form characteristic of the adult. Indeed, the correspondence between the bullae of young postnatal Tupaia and adult Ptilocercus applies even to such insignificant features as the small incisure found in the ventral meatal margin (fig. IV-42).

Tupaia glis MPIH 1961/11
(adult)

In the sectioned adult the entotympanic is entirely bony except for part of the ventral margin of the external auditory meatus. In some areas, particularly around the hypotympanic sinus, its bone is obviously lamellar in structure (fig. IV-39b). The entotympanic is almost entirely free of surrounding bones; there are no areas of synostosis with the alisphenoid, basisphenoid, or basioccipital. As already mentioned, the posterior extremity is fused to the CTPP; the entotympanic is also lightly fused to the squamosal in the area of the stylomastoid foramen. The tegmen tympani and superior part of the entotympanic display a small area of fusion in front of the foramen for the ramus superior of the stapedial artery (cf. figs. IV-3, IV-4).

An interesting condition is found along the ventral margin of the external auditory meatus, where highly irregular nodules of cartilage-like material line its aperture (fig. IV-39a,b). These nodules are continuous with the entotympanic; although the medial edge of the auricular cartilage lies very near the meatus, none of the nodules were fused to it. It is quite possible that these nodules represent unossified remnants of the entotympanic. On the other hand, they bear a certain resemblance to the so-called 'chondroid tissue' which is often found on the margins of the alveoli surrounding the teeth (SICHER and BHASKAR 1972:206). ENLOW (1962:83) states that

> this curious tissue is associated with localized regions which seem to require accelerated growth and yet which must provide anchorage and perhaps resistence to pressure....The cartilage-like cells appear to undergo direct conversion into osteocytes and become included in seemingly typical non-lamellar bone, although this supposition is not certain.

In this context, it should be noted that there is no layer of dense connective tissue separating this material from the bone of the entotympanic, unlike the case of the transition between the cartilage of the tube and the entotympanic in the same specimen (see 4.1.2; fig. IV-38).

These nodules seem to be a normal feature of the rim of the meatus in adult *Tupaia*, for they were found in a number of skulls which had not been vigorously cleaned of all soft tissue. In some cases they attain a rather large size, although none compare to the accessory cartilages or ossicles which have been described for Macroscelididae, Dasypodidae, or Rodentia (VAN KAMPEN 1905:557-558; VAN DER KLAAUW 1931:157; ALLEN 1904). Moreover, in some cases these cartilages are supposedly formed from the auricular cartilage, which is not the situation in _Tupaia_.

4.1.3.3 _Note on the Entotympanic of Ptilocercus_

Ptilocercus also possesses an entotympanic (LE GROS CLARK 1926), but it is smaller than in _Tupaia_ and has a different form.

Perhaps its most interesting feature is that it does not complete the anterior wall of the bulla, which is formed by the tympanic process of the alisphenoid instead (fig. IV-42; see also 4.1.9). There is a complete suture separating the two in the adult, as in elephant shrews (figs. V-2, V-3).

Comparison with macroscelideans suggests that the entotympanic of _Ptilocercus_ is a caudal rather than a rostral element. This raises difficulties with the evaluation of the entotympanic of _Tupaia_, which was considered to be a rostral entotympanic because it is primordially fused with the cartilage of the tube. This problem will not be settled until a separate investigation of bullar ontogeny in _Ptilocercus_ is made. In any event, there is no basis for suggesting that the anterior mass of cartilage found in young stages of _T. glis_ consists of both entotympanics and the cartilage of the tube, all indivisibly fused with one another.

4.1.4 TYMPANIC PROCESSES OF THE PETROSAL

4.1.4.1 _Caudal Tympanic Process of the Petrosal_

SPATZ (1966) has described a small CTPP which completes the posterior end of the auditory bulla in _Tupaia_. As noted in section

4.1.3, the CTPP fuses with the entotympanic while both are still cartilaginous; no suture passes between the two in the adult.

In young specimens (figs. IV-1, IV-21, IV-22, IV-23, IV-27), the CTPP is a minute lamella of cartilage situated alongside the posterolateral extremity of the presumptive middle ear. In respect of its position and relations, the tupaioid CTPP is more like that of certain insectivores than strepsirhine primates. It arcs from the distal end of the facial sulcus (near the site of the foramen stylomastoideum primitivum) and thence across a portion of the anteroventral surface of the pars canalicularis. Due to its roughly semicircular form, the CTPP encloses the posterior end of the presumptive tympanic cavity as defined by the fibrous membrane. However, it terminates well behind the apertura fossulae fenestrae cochleae instead of continuing medially along the processus recessus. Superficially, the tupaioid CTPP appears to have a disposition similar to that of the lateral and posterior sections of the PTPC described for *Microcebus murinus* (cf. fig. II-1). However, closer examination reveals an important difference. The lateral section of the CTPP of *Microcebus* originates from the posterior continuation of the crista parotica. In *Tupaia* there is a well-marked posterior continuation of the crista parotica also, but the CTPP is an entirely separate outgrowth which lies *medial* to it (figs. IV-22, IV-23).

There is also a principal difference in the relationship of the CTPP and the stapedius muscle. In strepsirhines, the CTPP completely surrounds the site of origin of this muscle, such that it lies within the confines of the middle ear from the outset (figs. II-2, II-30, III-1, III-12). In Tupaia, the CTPP lies medial to the stapedius; accordingly, the muscle must pass across the anterior end of the process in order to enter the tympanic cavity (fig. VI-21). In fig. IV-22 it can be seen that the stapedius is accommodated within a deep trough formed by the CTPP medially and the posterior continuation of the crista parotica laterally; this condition, which is quite insectivore-like (see fig. I-2), is retained throughout ontogeny (fig. IV-5) and is correspondingly different from the strepsirhine case.

The CTPP is both chondrified and ossified from the auditory capsule; there is no sign of its having an independent existence at any stage. The process is completely ossified by the nineteenth day after birth (figs. IV-36, IV-37).

Since there is no suture between the CTPP and the entotympanic in the adult, it is difficult to determine the extent of its participation in the mature bulla. However, it grows relatively slowly and undoubtedly forms only a small fraction of the external bullar wall in the adult (see fig. IV-5).

4.1.4.2 Rostral Tympanic Process of the Petrosal

There is no good evidence that a RTPP comparable to that of strepsirhines is formed in Tupaia. A low ridge is found on the ventral surface of the ossified promontory in MPIH 1964/10 (19 days old), but there is no sign of the intense osteoblastic activity which accompanies the production of the RTPP in lorises and lemurs. This ridge shows no relative increase in size in the sectioned adult specimen (fig. IV-11; see also fig. IV-4). On the whole, it appears that the function of this ridge is similar to that of the cristae of the sphenoid and occipital, i.e., to give purchase to the entotympanic bulla (see fig. IV-4 and 4.1.9). Although it arises from the promontory, it does not appear in the external wall of the bulla and does not fuse with the entotympanic.

4.1.5 ECTOTYMPANIC

4.1.5.1 Structure, Relations and Development

The ectotympanic maintains an anular form throughout ontogeny, which is supposedly a primitive trait (VAN KAMPEN 1905:357). As in the case of lemurs, the ectotympanic tends to retain its embryonic proportions as it grows.

The ectotympanic is already present in the youngest specimen (MPIH 1960/82a). At this stage, it consists of a complete semicircle of bone, more or less constant in thickness and without a well-defined sulcus for the tympanic membrane (fig. IV-7). The apex of the anterior crus is only very slightly broadened where the gonial and Meckel's cartilage pass over it. The medial margin of the ectotympanic is situated directly beneath the promontory, and the bone has no attachments to any other skeletal elements.

Active growth, as indicated by the concentration of osteoblasts and the condition of the periosteum, continues until the third week after birth. By this time, adult size has almost been reached. The ectotympanic is composed of the same type of nonlamellar, intermediate bone described for lemurs (see 2.1.4), and does not undergo any significant degree of remodelling between the nineteen-day and adult stages (fig. IV-10, IV-11).

In the adult, the posterior crus is fused to the squamosal only in the area where the chorda tympani passes through its canaliculus into the tympanic cavity. The posterior crus does not fuse with the entotympanic (figs. IV-40, IV-41) and the anterior crus has only a fibrous union with the squamosal in MPIH 1961/11 (adult). However, SABAN (1963:119) states that the latter two are fused in Tupaia. The only other element which fuses with the ectotympanic is the gonial (FLEISCHER 1973:147).

One other feature of the ectotympanic deserves mention. In adult tupaioids, a small process given off by the anterior crus passes through the cleft formed by the postglenoid process dorsally and the rim of the external auditory meatus ventrally (fig. IV-44). Among the sectioned specimens, this process was evident only in the adult stage (MPIH 1961/11), so no conclusion can be reached concerning its development. It is highly unlikely that it is a separate element, however, and it is definitely neither the gonial nor an ossified section of Meckel's cartilage. The process may have a support function, for the ectotympanic in the adult tree shrew is even 'freer' than it is in the adult lemur.

4.1.5.2 Inclination of the Ectotympanic

Inclination values for the ontogenetic series of *T. glis* (table 4-2) suggest that the rotation of the ectotympanic is mainly a postnatal event, for there is little displacement until after the eighth day. This may be correlated with the fact that the entotympanic cannot inflate to any degree until ossification begins.

The ventral hinge must operate somewhat differently than in lorises and lemurs (see 2.1.4.2 and 3.1.4.2), since the entotympanic never actually abuts the ectotympanic. The soft tissues between the ventral part of the ectotympanic and the intratympanic face of the entotympanic apparently keep the anulus firmly against the bullar rudiment, so that it rotates outwards concurrent with the laterad growth of the entotympanic (cf. figs. VI-9 and VI-10).

Although the anterior crus of the ectotympanic reposes within a shallow trough formed by the base of the anterior septum and the floor of the entotympanic (figs. IV-30, IV-39), it seems unlikely that the anterior process actively pushes the ectotympanic outwards during the pneumatization of the bulla. The reason for this is that the ectotympanic of *Ptilocercus* has about the same inclination value as *T. glis* in the adult stage, but the anterior septum is absent or vestigial in the former (see 4.3.2.1).

The adult value cited in table 4-2 (for MPIH 1961/11) is much lower than SABAN's (1963) estimate of 70° for *Tupaia* sp. The sectioned specimen is definitely mature, so either pronounced individual variation or strong species differences must exist among tupaioids for the angle

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of ectotympanic inclination.

4.1.6 RELATIONSHIP OF THE ECTOTYMPANIC AND ENTOTYMPANIC

4.1.6.1 Introduction

The modern Tupaioidea and Lemuriformes are unique[1] among mammals in possessing an unexpanded ectotympanic which is freely suspended 'within' the bulla. It is therefore hardly surprising that the aphaneric ectotympanic is often prominently listed in inventories of skeletal traits which suggest a proximate relationship between lemurs and tree shrews (e.g., WEBER 1927-28; LE GROS CLARK 1925, 1926, 1959, 1971; SABAN 1956-57; WERNER 1960a; BROERS 1963). However, this character cannot be evaluated in isolation. Ontogeny shows, for example, that the bulla which surrounds the ectotympanic is derived from the petrosal in lemurs and from the entotympanic in tree shrews. So basic a contrast cannot be ignored. Ontogeny also shows that the method of actual entotympanic enclosure by the bulla in lemurs differs from that found in tree shrews in some respects, as the next section will establish.

4.1.6.2 Development of the Ectotympanic-Entotympanic Relationship

Fortunately, the entire sequence of ontogenetic events leading to the enclosure of the ectotympanic by the entotympanic bulla is illustrated in the five sectioned specimens of _T_. _glis_. Briefly

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[1] Conditions in the marsupial mouse _Dasycercus_ _cristicaudata_ are not strictly comparable since the ectotympanic is broadened laterally and is connected to the external auditory meatus (cf. WOOD JONES and LAMBERT 1939).

Table 4-2

INCLINATION OF THE ECTOTYMPANIC IN YOUNG TUPAIOIDEA

Specimen No.	Angle of Inclination L	R	Average Inclination
Tupaia glis			
MPIH 1960/82a	34°	35°	34.5°
MPIH 1959/4	38°	37°	37.5°
MPIH 1960/77	36°	36°	36.0°
MPIH 1964/10	42°	43°	42.5°
MPIH 1961/11	54°	55°	54.5°

For computation of the angle of inclination, see note accompanying table 2-2.

stated, the petrosal plate of lemurs is able to grow around the ectotympanic because there is nothing to keep the bone territories in tandem once the petrosal plate enters its phase of rapid inflation. Sutural tissues are incompletely elaborated between the leading edge of the plate and the ectotympanic, with the result that the interface between them is inherently unstable (see 2.1.5). In Tupaia, the entotympanic is able to surround the ectotympanic because it differentiates and grows within a sheet of connective tissue (the fibrous membrane of the tympanic cavity) which lies ventral to the ectotympanic from the very beginning. In lemurs, the formation of sutural tissues is only partially completed; in tree shrews, it is not even initiated.

The development of the ectotympanic-entotympanic relationship is uncomplicated. The entotympanic can be considered to be definitely present in MPIH 1959/4 (newborn), and this specimen displays the earliest and least intimate condition of the relationship (fig. IV-1, IV-12). The caudal spur of entotympanic cartilage lies on the medial side of the ectotympanic at this stage. Yet it is predictable that the entotympanic must pass beneath the ectotympanic as its cartilage continues to develop within the fibrous membrane.

The fibrous membrane exhibits only a tenuous connexion with the periosteum of the ectotympanic. Tympanic mucoid tissue generally separates the two completely, as in the youngest specimen, MPIH 1960/82a (fig. IV-7). Even in sections where there appears to be a slight degree of contact (fig. IV-12), a thin strand of mucoid tissue can be discerned between the fibrous membrane and the periosteum of the ectotympanic under high magnification.

In MPIH 1960/77 (8 days old), the leading edge of the middle portion of the cartilaginous entotympanic has already passed beneath the ectotympanic (fig. IV-13). Again, compressed tracts of mucoid tissue separate the ectotympanic and entotympanic at sites of apparent contact. The same picture obtains in the slightly older MPIH 1964/10 (fig. IV-14).

The definitive condition of the ectotympanic-entotympanic relationship is illustrated in fig. IV-15. In the adult specimen (MPIH 1961/11) there was some disruption and shrinkage of soft tissues during processing. Even so, it is obvious that the ectotympanic is embedded within loose connective tissue and has no direct contact with the internal wall of the bulla or its periosteum.

The figures also conclusively demonstrate that there is no formation, at any stage, of sutural tissues equivalent to those found in lorises. Even in lemurs, the tympanic mucoid tissue is eventually expelled from the ectotympanic-petrosal plate interface, although no middle layer differentiates in that locality. In Tupaia, the mucoid tissue never completely withdraws from the site of closest approximation of the ectotympanic and entotympanic.

4.1.7 LINEA SEMICIRCULARIS

A linea semicircularis is present in Tupaiinae; in its form and disposition it closely resembles the similar structure described for lemurs (see 2.1.6). In the adult tree shrew, the linea consists of a small rampart of bone which juts into the tympanic cavity from the internal side of the lateral bullar wall; it is semicircular in form and lies directly beneath the ectotympanic (fig. IV-15). The linea was present in representative skulls of all genera save Ptilocercus, in which it is either absent or very poorly defined. It is likewise indistinct in the smaller tupaiids, such as Dendrogale (cf. Microcebus, 2.1.6).

Its disposition can be easily defined by external inspection of the adult bulla. The linea is responsible for the sharp, arc-like boundary between the opaque, vesiculated bone of the meatal region and the semitranslucent, lamellar bone which forms the remainder of the entotympanic.

In lemurs, the linea appears to form from the ventral enlargment found in young stages, although this is not certain. In Tupaia this cannot be the case since no ventral enlargment appears at any stage of entotympanic ontogeny. However, the linea serves the same functional purpose in both groups, i.e., the accommodation of the soft tissues in which the 'free' ectotympanic is seated.

The linea semicircularis develops late in bullar ontogeny, concurrently with the formation of the definitive external auditory meatus. In MPIH 1964/10 (19 days old) it is no more than an indistinct ridge restricted to the anterior part of the bulla (fig. IV-34). In the adult specimen (MPIH 1961/11) it can be traced across almost the entire medial face of the lateral bullar wall (figs. IV-11, IV-15).

There are no projecting outgrowths on the meatal lip in adult Tupaiidae (cf. conditions in some lemurs; section 2.1.6 and CARTMILL 1975).

4.1.8 'ANULUS MEMBRANE'

A number of authors have asserted that an 'anulus membrane' connects the ectotympanic to the lateral bullar wall in tupaioids (e.g., WINGE 1892 [1941]; LE GROS CLARK 1959; SABAN 1956-57, 1963). It may be mentioned at the outset that, just as in lemurs, there is no such membrane—at least as an entity separate from either the lining of the tympanic cavity or the skin of the membranous meatus (see 2.1.7).

In the sectioned adult (MPIH 1961/11), the ectotympanic is loosely situated in a trough formed by the linea semicircularis and the internal face of the bullar wall (fig. IV-15). The epithelium of the tympanic mucosa, which lines the intratympanic surfaces of the bulla, passes from the linea to the ectotympanic and thence to the tympanic membrane (of which it forms the mucosal stratum). Similarly, the skin forming the membranous meatus passes down the bullar wall (fig. IV-39a) to the ectotympanic, which is embedded in its substance, and thence to the tympanic membrane (of which it forms the cutaneous stratum). These are the only relevant soft tissues associated with the ectotympanic. The only pronounced difference from the lemuriform condition is that the dermis of the membranous meatus is not nearly so hypertrophied in Tupaia (fig. II-13; see also VAN DER KLAAUW 1931:199).

SABAN (1956-57:65; 1963:119) describes the 'anulus membrane' as being "cartilaginous", and lists it as one of the shared osteological characteristics of lemurs and tree shrews. Just as in Lemur (see 2.1.7), neither the tympanic mucosa nor the 'intrabullar' portion of the membranous meatus show any evidence of cartilage (see also CARTMILL 1975:333, fn.).

A peculiarity of the tupaioid external auditory meatus which is not seen in lemurs is the presence of cartilage-like nodules along the ventral margin of its aperture (see 4.1.3 and fig. IV-39a,b). Yet the nodules (whatever their method of histogenesis) were never seen to extend into the recessus meatus or have any association with the ectotympanic.

As for special lemur-tree shrew similarities with respect to the soft tissues binding the ectotympanic to the bullar wall, the association of the ectotympanic with the mucosa and the membranous meatus could hardly be other than close in both groups, given that the medial and lateral strata of the tympanic membrane are formed by these tissues in all mammals.

4.1.9 OTHER TYMPANIC PROCESSES

Only the entotympanic and the CTPP take part in the construction of the bullar walls in Tupaiinae.[1]

In Ptilocercus, however, there is an additional component, a tympanic process of the alisphenoid (fig. IV-42; GREGORY 1910:272, 274).

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[1] The CTPP is probably present in Ptilocercus, although this remains to be proven by appropriate developmental studies.

I had the opportunity to examine the same skull of Ptilocercus lowii (USNM 112611) which GREGORY (1910) described and illustrated in his monograph. Some adherent soft tissue remained in the groove which marks the structural boundary between the body of the alisphenoid and this process. With further cleaning, the depth of the groove became very apparent (fig. IV-42). However, the groove does not appear to be a suture, and accordingly GREGORY's evaluation of the process as an alisphenoidal outgrowth is doubtless correct.

VAN DER KLAAUW (1931:249) offers a different interpretation:

> According to Gregory....the marsupial-like developed alisphenoid wing of Ptilocercus is more primitive than the smaller one of Tupaia. This point now appears in another light, since I found....that an important part of the alisphenoid bulla in Macroscelididae, namely the part on the medial side of the Eustachian tube, is not formed by the alisphenoid but is a rostral entotympanic.

My observations on E. fuscipes and E. rozeti suggest that VAN DER KLAAUW is probably mistaken in believing that an ossified rostral entotympanic contributes to the tympanic process which lies medial to the tympanic aperture for the auditory tube (see 5.1.9). I see no good reason at this point for considering the bony covering of the auditory tube in Ptilocercus as other than a tympanic process of the alisphenoid, although its presence does complicate a decision concerning which of the two entotympanics is present in Tupaioidea (see 4.1.3.3).

In *Tupaia*, conditions are considerably different. There is a slight ridge which buttresses the anterior wall of the bulla between the foramen ovale and the postglenoid process (fig. IV-4). VAN KAMPEN (1905) ignored this ridge because it does not actually take part in the bulla, but GREGORY (1910) styled it as a reduced tympanic wing (process) of the alisphenoid in obvious reference to the large process found in *Ptilocercus*. In the course of his study, SPATZ (1966) noted that a low continuous crest externally surrounds the anterior and medial walls of the entotympanic bulla. Participating in this crest are small outgrowths of the squamosal, alisphenoid, basisphenoid, basioccipital, and exoccipital. Some would regard these ridges as tympanic processes--rudimentary or vestigial, yet nonetheless the homologues of processes found in some insectivores and marsupials. In SPATZ' view, however, these 'cristae' are independent acquisitions of tree shrews, developed in order to provide support for the entotympanic bulla.

It is always difficult to know how to evaluate what appear to be vestigial structures, and this case is no exception. On the balance, my own feeling is that SPATZ' (1966) appraisal is the best interim analysis. Accordingly, his neutral term 'cristae' will be employed to refer to the outgrowths surrounding the tupaiine bulla (fig. IV-4).

The cristae are indistinct even in the adult stage (figs. IV-4, IV-11). The one facing the anterior surface of the bulla, which is mostly formed by the entoglenoid of the squamosal with a small alisphenoidal contribution, is the best developed (cf. the small outgrowth in the same position in strepsirhines; sections 2.1.8, 3.1.6).

The pterygoid bone is still independent of the alisphenoid in the near-term fetus (MPIH 1960/82a) and lies above the anterior extremity of the anterior mass of cartilage (fig. IV-16). The pterygoid laminae do not reach the anterior surface of the bulla in the adult, although in the adult a fibrous ligament can be identified stretching between the lateral pterygoid lamina (of the alisphenoid) and the bullar wall.

4.2 DORSAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

The contributions of various bones to the roof of the tympanic cavity in the adult are illustrated in figs. IV-3 and IV-4. Anteriorly, the superior part of the entotympanic forms the rooves of diverticula D_1 and D_2. Actually, the entotympanic provides a 'second' roof for the rostral section of the roof of the middle ear, for it is reflected over almost the entire extent of the large epitympanic wing of the sphenoid. The visible portion of the epitympanic wing is restricted to a small loculus situated directly in front of the tegmen tympani. The entotympanic also hides a small epitympanic wing of the petrosal which arises from the anterior pole of the promontory. This wing is not at all like that of lemurs and instead resembles the slight process found in the same place in certain insectivores. The epitympanic wing is deeply grooved by the promontorial artery before that vessel passes into the cranial cavity.

The squamosal makes almost no contribution to the roof of the epitympanic recess and the petrosquamous suture cannot be seen from the ventral aspect.

4.2.1 TEGMEN TYMPANI, EPITYMPANIC WING OF THE PETROSAL, AND REICHERT'S CARTILAGE

4.2.1.1 Tegmen Tympani and Epitympanic Wing of the Petrosal

SPATZ (1964:393) has observed that the tegmen tympani of Tupaia is much larger than in any 'insectivore' (except Elephantulus) and approaches that of prosimians in size.

As always, the tegmen originates from the anterolateral border of the pars canalicularis and covers the fossa incudis. However, as in primates, the tegmen also continues to grow anteriorly and forms a roof over the entire ossicular chain.

In the two youngest specimens (MPIH 1960/82a and MPIH 1959/4) the tegmen is an ample bar of cartilage which possesses, as its most prominent feature, a capacious foramen for the ramus superior of the stapedial artery. It shows signs of incipient ossification posteromedially where it springs from the pars canalicularis. The center of ossification lies slightly further posteriorly in the hind wall of the cavum supracochleare. The tegmen ranges anterolaterally from its origin, leaving a very broad gap--the piriform fenestra--between its medial margin and the promontory (fig. IV-7).

The posterior part of the tegmen tympani is unremarkable. It displays a fairly prominent sulcus facialis which joins the crista parotica posteriorly. The epitympanic crest, which defines the medial wall of the epitympanic recess, is entirely given over to the support of a relatively enormous canal for the stapedial artery (fig. IV-25). Medially, a tensor fossa is absent because this muscle is not present in *T. glis* (see 4.4.1).

Anteriorly, the tegmen ends on a parallel with the anterior pole of the promontory, over the proximal part of Meckel's cartilage. It is still widely separated from the anterior mass of cartilage (cartilage of the tube + entotympanic). Since the tympanic wing of the sphenoid covers only the rostral part of the piriform fenestra in the newborn specimen, it follows that the roof of the middle ear is still partly membranous at birth (fig. IV-2, IV-8). As usual, the lateral margin of the tegmen abuts the squamosal, and together these two elements define a shallow epitympanic recess.

In the week-old specimen (MPIH 1960/77), the leading edge of the tegmen is fused with the anterior mass of cartilage, forming the entotympanic-tegminal commissure (see 4.1.3). Ossification has proceeded deep into the base of the tegmen and downwards from there into the cartilage surrounding the stapedial artery.

In MPIH 1964/10 (19 days old) the tegmen is completely ossified except at the site of the entotympanic-tegminal commissure. The lateral margin of the tegmen is completely bony, but it is not fused to the squamosal.

In the adult specimen (MPIH 1961/11) ossification of the tegmen is complete. The bone of the tegmen is continuous with that of the entotympanic in a small region around the foramen for the ramus superior. The piriform fenestra has been obliterated and the tegmen extends to the level of the anterior pole of the promontory (but not beyond it; see fig. IV-4).

The tegmen tympani is evidently similar in size in Ptilocercus, judging from LE GROS CLARK's illustration (1926:1196, text-fig. 10). The constitution of the roof of the tympanic cavity in other tupaioids could not be determined without breaking away the enclosing bullae, but there is no reason to suspect that they differ from Tupaia.

4.2.1.2 Reichert's Cartilage

There is nothing remarkable about Reichert's cartilage. As usual, it extends ventrally from the crista parotica on the sidewall of the auditory capsule. SPRAGUE (1944) has investigated the hyoid apparatus of adult tree shrews and found that the most cranial part of the hyoid, the tympanohyal, is situated within a canal (vagina processi hyoidei) in the entotympanic (fig. IV-41). The tympanohyal is also present in Ptilocercus, and in both genera it is protrematic in position (i.e., is attached to the petrosal anterior to the point where the facial nerve leaves the auditory capsule).

4.2.2 EPITYMPANIC WING OF THE SPHENOID

All authors who have made first-hand studies of the roof of the tympanic cavity are agreed that a dorsal outgrowth of the sphenoid participates in it. Dissection of the roof establishes that the epitympanic wing is actually very large in the adult Tupaia. However, it is almost completely hidden by the broad superior part of the entotympanic (cf. figs. IV-3 and IV-4).

The development of the epitympanic wing is uncomplicated. It is an intramembranous prolongation of the sphenoid (mostly of its alisphenoid portion) and it initially fills much of the rostral part of the wide piriform fenestra between the promontory and the tegmen tympani (fig. IV-1). The foramen ovale, when completed, lies entirely within the epitympanic wing near its junction with the body of the alisphenoid (fig. IV-4). However, since the anterior part of the entotympanic is so closely appressed to the sphenoid, external inspection of the adult without dissection gives the impression that both elements together form the foramen ovale. The epitympanic wing does not fuse with any of the other bones participating in the cranial wall and is easily separated from the entotympanic in the adult skull. The promontorial artery passes into the cranial cavity through the large cleft between the hind edge of the wing and the anterior pole of the promontory (fig. IV-4).

LE GROS CLARK (1926:1197) states that "a much larger proportion of the roof of the tympanic cavity is formed by the alisphenoid in Ptilocercus than in Tupaia". This comment should be understood in relation to the different method of construction of the roof of the tympanic cavity in Tupaiinae. In Ptilocercus, the entotympanic does not cover the 'area A' defined by LE GROS CLARK (equivalent to the lateral diverticulum, D_1, of SABAN 1963), as it does in Tupaia. Accordingly, while a much larger proportion of the epitympanic wing is visible in Ptilocercus, the wing is not relatively or absolutely larger than in Tupaia.

4.2.3 EPITYMPANIC WING OF THE SQUAMOSAL

In Tupaia, the squamosal forms the lateral walls of the tympanic cavity, epitympanic recess and fossa incudis, but it does not participate in their rooves to any significant extent. The epitympanic wing of the squamosal, which forms a section of the lateral part of the roof of the middle-ear cavity in strepsirhines, is thus almost entirely absent in Tupaia (figs. IV-10, IV-11). The squamosal is not pneumatized to any important degree in the adult (SABAN 1963).

The squamosal develops as a typical membrane bone, as usual. Secondary cartilage is not evident in the region of the glenoid cavity and postglenoid process until after birth. The posterior margin of the squamosal covers only a small part of the pars canalicularis; thus this part of the auditory capsule appears as part of the external wall of the skull in the adult (in Ptilocercus also; see LE GROS CLARK 1926).

The articulation of the crura of the ectotympanic with the squamosal has already been described (see 4.1.5).

4.3 PRINCIPAL SPACES AND SEPTA OF THE MIDDLE EAR

Pneumatization of the bones comprising the walls of the middle ear results in the formation of two major spaces which broadly communicate with the tympanic cavity: the hypotympanic sinus and the epitympanic recess. There is, in addition, an insignificant diverticulum which corresponds to the aditus of the mastoid cavity of strepsirhines. A number of minute cellules are encountered in various positions in the adult; these are fully described by SABAN (1963, 1964).

Although the septal content of the tupaiine middle ear resembles that of lemurs to some degree, the septa of the two groups are probably not homologous (see table 4-3).

4.3.1 PRINCIPAL SPACES

4.3.1.1 Hypotympanic Sinus

The hypotympanic sinus attains large size, as in lemurs. According to SABAN (1956-57, 1963, 1964), the tupaiine hypotympanic sinus can be divided into three diverticula (D_1, D_2 and D_3) which are equivalent to the spaces occupying similar positions in strepsirhines (see 2.3.1.1 and 3.3.1.1). Diverticulum D_3 is considered here to be part of the true tympanic cavity instead of the hypotympanic sinus (see 2.3.1.1), but it will be described under this heading for convenience.

Diverticula D_1 and D_2 are separated rostrally by the anterior septum. Diverticulum D_1, into which the tubal canal passes, is situated on the lateral side of the anterior septum (fig. IV-3). The small lateral secondary septum (fig. IV-3) defines another, very small innominate diverticulum in advance of the anterior pole of the promontory. This diverticulum cannot be seen from the ventral aspect (fig. IV-3). Diverticulum D_2 is much larger than D_1 and extends from the anteromedial extremity of the middle ear cavity to the carotid canal, medial to the position of the ectotympanic. Diverticulum D_3 lies behind the fossula fenestrae cochleae and is bounded medially by a minute posterior septum on the carotid canal.

Diverticula D_1 and D_2 can be identified as separate invaginations of the anterior mass of cartilage (cartilage of the tube + entotympanic) in the youngest specimen (MPIH 1960/82a). The small innominate diverticulum develops as soon as the anterior mass begins its caudal prolongation (fig. IV-29).

An anterior-posterior gradient in the formation of the hypotympanic sinus and therewith the inflation of the bulla is much more obvious than in lemurs, since the entotympanic is preformed in cartilage. In MPIH 1964/10 diverticula D_1 and D_2 have already attained a large volume rostrally where the entotympanic is extensively ossified and undergoing pneumatization. Posteriorly, however, the hypotympanic sinus is barely indicated since the entotympanic is still cartilaginous.

4.3.1.2 Epitympanic Recess

The roof of the epitympanic recess is almost entirely formed by the tegmen tympani (see 4.2.1) and attains a fairly large size, as in lemurs (fig. IV-11). It is bounded posteriorly by the distal part of the facial canal and the prominence of the lateral semicircular canal and anteromedially by the stapedial canal and its associated epitympanic crest (fig. IV-3). The recess evidently expands in size for a period after birth, for it is very small in the neonate and week-old specimen and only slightly deeper in the nineteen-day old specimen.

There is no equivalent of the supracochlear cavity of lorises.

4.3.1.3 Mastoid Cavity

SABAN (1963:135) records that the mastoid process (= post-tympanic process) is inflated by a large cellule which might be compared to the antrum of the mastoid. However, this cellule is said to lack any communication with the epitympanic recess.

Cross-sections of the adult specimen of T. glis (MPIH 1961/11) show, however, that the adital part of the mastoid cavity can be distinguished in the usual place (i.e., in the lateral wall of pars canalicularis above the lateral semicircular canal; see figs. IV-40, IV-41). This indentation does not lead into a true antral cavity and does extend into the squamosal.

4.3.2 PRINCIPAL SEPTA

4.3.2.1 Anterior Septum

The anterior septum is formed by the entotympanic alone. Its rostral part is identifiable in the near-term fetus (fig. IV-17); the rest of it develops pari passu with the caudad growth of the entotympanic. It reaches the anterior pole of the promontory after the first week of postnatal life, and at the same time encloses the distal portion of the promontorial artery (figs. IV-4, IV-30).

On present evidence, it appears that the center of ossification for the entotympanic originates within the superior part of the anterior septum (see 4.1.3.2).

The anterior septum is not wholly absent in Ptilocercus in the sense that there is a small ridge occupying the equivalent position in the rostral part of the middle ear cavity of that genus. However, it is very low and may represent no more than the slightly-raised margin of the entotympanic. The superior part of the entotympanic is deficient compared to that of Tupaia, for it does not cover diverticulum D_1 in Ptilocercus (see LE GROS CLARK 1926:1196, text-fig. 10).

4.3.2.2 Posterior Septum

The posterior septum is so inconsiderable that it is difficult to separate it anatomically from the carotid canal. Sometimes it is completely absent, as in the specimen used for figs. IV-3 and IV-4. It is formed by the entotympanic, like the rest of the carotid canal (see 4.4.2).

4.3.2.3 Other Septa

In the adult, the stapedial canal is suspended from the roof of the tympanic cavity by a bony rampart (fig. IV-11). This rampart is formed by the tegmen tympani and may be regarded as the equivalent of the epitympanic crest of strepsirhines.

The medial secondary septum transmits a small vein, as in lemurs (although it is formed by the entotympanic, not the petrosal, in T. glis).

The lateral secondary septum can be identified early in bullar ontogeny (fig. IV-29). Like the anterior septum, it forms

Table 4-3

PRINCIPAL SEPTA OF THE MIDDLE EAR
(TUPAIOIDEA)

Terms Employed by SABAN (1956-57)	Terms Employed in this Study	Origin and Position
septum principal (longitudinal)	anterior septum	entotympanic parasagittally, from anterior pole of promontory to tubal canal
[not recognized]	epitympanic crest	petrosal; on tegmen tympani runs along anterior limit of epitympanic recess (supports stapedial canal)
(petit) septum transversal	medial secondary septum	entotympanic medially, from anterior pole of promontory to inner surface of medial wall of bulla (carries small vein)
septum secondaire	lateral secondary septum	entotympanic anterolaterally, from anterior septum
(petit) septum longitudinal	posterior septum	entotympanic (supports canal for internal carotid a.)

without any initial relationship to blood vessels.

4.3.2.4 Septal Homologies of Tree Shrews and Lemurs

SABAN (1956-57:94) argues that two of the cranial features suggesting a proximate relationship between lemurs and tree shrews are the enlargement of the hypotympanic sinus and the similarity in the disposition of the septa bounding the diverticula of the bulla. The first character may be accepted as descriptive of conditions in both groups; whether it signifies much is doubtful, since a large hypotympanic sinus is found in many mammals (VAN DER KLAAUW 1931; VAN VALEN 1965).

In order for the second character to have any force, the septa themselves must be homologous, and this is questionable. Since SABAN made his studies under the misapprehension that the tupaioid bulla was a petrosal derivative, it is understandable that he might regard the septa of lemurs and tree shrews as homologous in origin as well as position. However, since there can now be no question that the bulla is mostly entotympanic in origin, it is necessary to re-evaluate the supposed equivalency of these septa.

The most important homological question concerns the anterior septum. Lemurs and tree shrews are said to be similar in the 'incompleteness' of the anterior septum (i.e., the septum does not completely divide the middle ear cavity) and correspondingly different from the lorisiform condition (in which the misidentified 'septum longitudinal' is complete). However, the anterior septa have utterly different origins in the two former groups. In lemurs, the septum is formed by the everted margins of the tegmen tympani and epitympanic wing of the petrosal along the remnant part of the piriform fenestra. In *Tupaia*, the septum is entirely formed by the entotympanic. Moreover, the whole construction of the anterior part of the dorsal wall differs considerably from that of lemurs. The piriform fenestra can be said to remain widely open in the sense that the wings bounding this dehiscence in other mammals are not in close contact in the adult. This is not evident unless the superior part of the entotympanic is stripped away (fig. IV-4). Since the tegmen tympani and small epitympanic wing of the petrosal do not even meet in front of the anterior pole of the promontory (fig. IV-4), they obviously cannot form an anterior septum like that of lemurs.

The posterior septum and carotid canal are formed by the entotympanic alone, even though the CTPP is present in *Tupaia*. The medial and lateral secondary septa also have an entotympanic origin.

Thus, even if one still takes the view that the entotympanic of tree shrews is in some sense the homologue of the petrosal plate of lemurs (see 8.5.5), it is still not possible to assume that the major and minor septa of the two groups are equivalent--at least from an ontogenetic perspective. The anterior septum of tree shrews is definitely not the homologue of that of lemurs as it has no relation to the tegmen tympani or the superior wing of the petrosal. The formation of the medial secondary and posterior septa are best interpreted as further examples of the prediliction of tree shrews to form bony processes and tubes for the blood vessels of the auditory region--a prediliction shared not only with lemurs but with talpids, erinaceids, chrysochlorids, pantolestids, and others (VAN DER KLAAUW 1931; VAN VALEN 1965).

This leaves only the lateral secondary septum (which is not represented at all in lemurs) and the epitympanic crest (for which homology is likely). On the whole, one must conclude that the septal content of the middle ears of tree shrews and lemurs provides no significant evidence for close relationship.

4.4 MUSCLES, ARTERIES AND NERVES OF THE MIDDLE EAR

4.4.1 OSSICULAR MUSCLES

All of the sectioned specimens of T. glis used for this study display complete bilateral absence of the tensor tympani (see also SPATZ 1964). This is curious, for SABAN (1963:127, 321) gives a detailed description of this muscle for Tupaia sp. According to SABAN, the tensor tympani takes origin from the area of the Glaserian fissure (gouttière malléolaire) instead of the lateral wall of the promontory (as in Lemuriformes). Close examination of the same area in all specimens, including the adult, failed to reveal any sign of this muscle. SABAN (1963) does not name the species of Tupaia in which he found the tensor tympani, and perhaps there are species differences for this particular muscle. It may also be mentioned that the processes muscularis of the malleus, into which the tensor tympani usually inserts, is said to be absent in T. glis (FLEISCHER 1973) and Ptilocercus lowii (LE GROS CLARK 1926).

The stapedius muscle was present in all specimens. Unlike strepsirhines, the fibres of this muscle take origin from the external wall of the auditory capsule because the stapedius fossa is not incorporated into the middle ear (see 4.1.3 and 4.1.4). An extra-tympanic origin of the stapedius is characteristic of most insectivores. In the adult, the stapedius passes into the tympanic cavity through a bony tube (pyramidal canal; SABAN 1963:128) in order to insert on the stapes (figs. IV-40, IV-41). The muscle is supplied by the stapedius branch of the facial.

There was no element of Paaw in the specimens available to me, although HINCHCLIFFE and PYE (1969:281) found it to be present (on one side only).

4.4.2 ARTERIES

4.4.2.1 Introduction

LE GROS CLARK (1925), SABAN (1963), STEUERWALD (1969), and BUGGE (1974) have elucidated most of the significant morphological aspects of carotid circulation in *Tupaia*. LE GROS CLARK (1926) has also described the tympanic branches of the carotid in *Ptilocercus*, but the carotid systems of other tree shrews have not yet been investigated. Nonetheless, on the basis of present evidence, all tupaioids probably conform fairly closely to the pattern illustrated in fig. IV-6.

4.4.2.2 Stem and Major Tympanic Branches of the Internal Carotid Artery

In the sectioned specimens, the vessels constituting the tympanic section of the carotid system differ from the well known conditions of the adult only in luminal calibre and degree of enclosure by cartilaginous or bony canals. Accordingly, only the ramus inferior, which has not been properly recognized in most studies, requires more than a summary description.

The internal carotid enters the middle ear cavity postero-medially in association with the stem of the internal carotid nerve and the tiny inferior tympanic artery (fig. IV-6).

After passing through the posterior carotid foramen the internal carotid gains the floor of the promontory in advance of the ventral lip of the apertura fossulae fenestrae cochleae. After a course of a few millimeters it bifurcates into the proximal stapedial and promontorial arteries.

The promontorial branch leaves the internal carotid at a sharp angle and travels across the ventral surface of the promontory towards the posterior margin of the anterior septum. It leaves the tympanic cavity through the anterior carotid foramen (fig. IV-4) in order to gain the circulus arteriosus; there is no vidian branch at any stage.

From its origin, the stapedial artery passes upwards through the obturator foramen of the stapes, then strikes anteriorly along the roof of the tympanic cavity. It passes into the cranial cavity through the foramen for the ramus superior, which is located in the anterolateral extremity of the tegmen tympani (fig. IV-4). Within this foramen it bifurcates into a ramus superior, which is of the same calibre as the parent vessel, and a much smaller ramus inferior. The ramus superior has long been known, but the existence of a ramus interior in Tupaia has usually been denied. Accordingly, this vessel requires a separate treatment.

4.4.2.3 Ramus Inferior of the Stapedial Artery

It may be stated at the outset that the ramus inferior is present in young stages of *T. glis* and persists into the adult stage as a slender anastomotic vessel running between the proximal stapedial and 'internal' maxillary arteries. The question of whether the ramus inferior is present or absent in *Tupaia* has undergone several vicissitudes. Since this vessel has some significance for phylogenetic interpretations, it will be useful to present (and emend) the findings of other authors.

The earliest observation appears to be that of HYRTL (1845; cited by GREGORY 1910), who maintained that the artery was present and large.

This was challenged by LE GROS CLARK (1925), who concluded that the ramus inferior should be considered as either absent or vestigial. Although he found twigs of this artery on one side of an immature specimen of *Tupaia* sp., he evidently felt that such vestiges could not be validly regarded as the full homologue of the ramus inferior. In sharp contrast, he (1926:1234) found a well-developed ramus inferior in Ptilocercus. In line with his general conclusions about this genus, he regarded the presence of this vessel as a primitive retention.

SABAN (1963:138, fn) has complicated the issue by suggesting that the ramus inferior of Ptilocercus may be the homologue of a completely different vessel, the anterior tympanic artery. He (1963: 139, fig. 26A) illustrates (for Tupaia, not for Ptilocercus) this artery as a small twig of the 'internal' maxillary which has no connexion with the proximal stapedial. SABAN's implication, then, is that the ramus inferior is completely absent in all tupaioids, not just the Tupaiinae.

In a careful and detailed study of latex-injected preparations of adult specimens of T. glis, STEUERWALD (1969:127, 133) found that an anastomotic branch of the proximal stapedial to the internal maxillary was consistently present. By its course and relations this vessel could only be a true ramus inferior.

However, BUGGE (1972, 1974:32), using an acrylic-resin injection and corrosion technique, has reiterated the generally held view that the 'distal part of the stapedial' (i.e., the ramus inferior) is obliterated in T. glis.

My observations on the five sectioned specimens of T. glis used for this study confirm STEUERWALD's (1969) findings. The vessel is always small and often minute, ranging from less than one-half to approximately one-ninth the luminal diameter of the proximal stapedial. The ramus inferior cannot be securely identified in the adult specimen (MPIH 1961/11) because of tissue damage during histological processing. However, STEUERWALD's (1969) study demonstrates that this vessel is normally present in the adult as well.

The ramus inferior is quite short and takes a somewhat unusual route compared to the course of this vessel in insectivores. As is typically the case in mammals possessing this ramus, the artery arises from the proximal stapedial as the latter enters the foramen for the ramus superior. However, instead of traversing the ventral surface of the roof of the tympanic cavity as usual, the vessel travels within the cranial wall, between the superior part of the entotympanic and the epitympanic wing of the sphenoid (figs. IV-28, IV-29, IV-33). Accordingly, it is not visible from the ventral aspect without dissection of the roof of the tympanic cavity, which explains why it has so often been missed. It continues in an anteromedial direction, lateral to the lesser petrosal nerve, dorsomedial to the chorda tympani, and ventromedial to the squamoso-alisphenoid suture. It meets the 'internal' maxillary at the rear of the glenoid fossa, lateral to the foramen ovale. This corresponds well to LE GROS CLARK's (1926) description of the ramus inferior of Ptilocercus, with the difference that the route of this artery is visible ventrally in this genus because the entotympanic does not extend across the epitympanic wing of the alisphenoid in 'area A' (i.e., diverticulum D_1; see 4.1.3).

Whether it is proper to speak of the ramus inferior as highly reduced in Tupaia is arguable. In all cases in which the vessel could be traced in my material, the anastomotic connexion was complete in the sense that the ramus extended between the proximal stapedial and 'internal' maxillary without interruption or obliteration. Additionally, the vessel is also small in Ptilocercus; it is about one-third the diameter of the proximal stapedial according to LE GROS CLARK (1926:1234). The involuted twigs found by LE GROS CLARK (1925), and perhaps also SABAN's "anterior tympanic artery", suggest that the ramus inferior may be partly obliterated in some individuals of Tupaia. However, without further data it cannot be said that these cases represent anything more than individual variation.

On the other hand, the ramus inferior in both Ptilocercus and Tupaia is much smaller than in such insectivores as Erinaceus (see 6.4.2.2).

The ramus inferior does not travel within a canal as it passes through the fibrous tissue uniting the entotympanic and epitympanic wing of the sphenoid. Since it is small as well, it is probably very difficult to trace in adult skulls, even with careful dissection. It was not possible to determine whether the ramus is typically present in other Tupaiidae because this would involve breaking away the bullae. If it is, it must become external within or adjacent to the Glaserian fissure. There are several minute foramina in this region in adult tupaioids, but it would be impossible to say which (if any) accommodated the ramus inferior (see fig. IV-5). On the balance, however, there is now good reason to believe that this vessel is present in all tree shrews, not just Ptilocercus.

4.4.2.4 Relative Size of the Promontorial and Stapedial Arteries

LE GROS CLARK (1926:1234) asserts that the promontorial artery of *Tupaia* is no more than one-third the diameter of the proximal stapedial artery, and regarded this reduction as a lemurine feature. He contrasted this condition with what he regarded as the more primitive one of *Ptilocercus*, where the vessels are nearly equal in calibre.

STEUERWALD (1969:131) objects that in her specimen of *T. glis* the two vessels are nearly equal in diameter, the stapedial artery being only slightly larger at most.

The relative sizes of the two arteries is of some physiological as well as phylogenetic interest. Reduction implies that the vertebral-basilar arteries have assumed a greater importance for the blood supply of the brain. This is indeed a lemurine specialization, although it is found in other mammals as well. Non-reduction implies that the internal carotid system remains important to cerebral irrigation. This is a more frequent condition than the previous one, and is notably common among insectivores. Since LE GROS CLARK was chiefly concerned with demonstrating tupaioid-lemurine affinities, it is important to know whether tree shrews and lemurs are truly similar for reduction of the promontorial branch as he maintained.

In section 2.4.2 it was noted that the promontorial artery is indeed reduced in *L. catta* (although it probably rarely obliterated even in this species, contra BUGGE 1974). In the sectioned adult specimen of *T. glis* the promontorial and stapedial arteries were poorly preserved, but the ratio of the inside diameters of their bony canals was about 4:5. This is more in accord with STEUERWALD's observation than LE GROS CLARK's. The rest of the specimens of *T. glis* show no definite ontogenetic sequence towards diminution of the promontorial branch. In the youngest specimen the promontorial branch appears to be slightly larger than the proximal stapedial. In the older specimens the stapedial is larger, but usually not by very much. On the whole, the evidence is not strong for any significant decrease in the importance of the internal carotid system for the supply of the brain in *Tupaia*.

4.4.2.5 Canals

The internal carotid, promontorial and stapedial arteries are enclosed in bony tubes in the adult *T. glis* and other tupaioids. Details of their construction and ontogeny have not been previously reported so a short summary is presented below.

The canal for the stapedial is the first to form, and it does so in a peculiar manner. Cartilage derived from the tegmen tympani evidently migrates along the entire length of the artery except for the small area where it perforates the stapes. Part of this canal is already present in MPIH 1960/82a (near-term fetus); there is a clear histological break between the cartilage of the canal and that of the promontory upon which it rests (fig. IV-20). The same break is identifiable in the week-old specimen (MPIH 1960/77;

fig. IV-9). Another peculiarity of the development of this canal is that the tegminal cartilage does not migrate beyond the point of bifurcation of the internal carotid. That is, it does not cover either the internal carotid itself or the promontorial artery.

The canal for the internal carotid artery is mostly derived from the entotympanic. This element, while still cartilaginous, grows along the internal carotid to its point of bifurcation in a manner analogous to the envelopment of the stapedial artery by the cartilage of the tegmen tympani. The entotympanic forms the floor and sidewalls of the carotid canal, but the promontory forms its roof (fig. IV-35).

The canal for the promontorial artery develops last, and most of it arises as a periosteal outgrowth of the ossified promontory. The distal part of the artery, where it perforates the roof of the tympanic cavity in front of the anterior pole of the promontory, is covered by the hind edge of the anterior septum (which is formed from the entotympanic; see fig. IV-3 and IV-4).

Thus the boundaries of the canals conform remarkably well to the anatomical divisions of the tympanic part of the internal carotid system. In the adult, the canals are inseparably fused to one another at the site of bifurcation of the internal carotid.

The canals are often described as 'complete' (e.g., VAN KAMPEN 1905:450), but this is not entirely the case. The stapedial canal shows a small fenestration where it passes through the stapes, as already noted. The promontorial canal, too, also shows a variable degree of fenestration in the different species of Tupaiinae. There is typically a small fenestration immediately behind the anterior septum (fig. IV-3). For some reason, fenestrations of considerable size are more common in the smaller species, such as Dendrogale melanura, T. gracilis and T. minor. The canals are always complete in Ptilocercus, which can be correlated with the fact that the bone forming them is thicker.

The reason for the appearance of these fenestrations of the promontorial canal is developmental, in the sense that the canal develops late and grows very slowly around the artery. For example, the canal is still only half-formed in the nineteen-day old specimen (fig. IV-10).

4.4.2.6 Foramina

(1) Posterior Carotid Foramen

There are some differences in the diameter of the posterior carotid foramen in the adult, which are no doubt related to the gross size of the animal and therewith the internal carotid. The foramen of the smallest genus (Dendrogale) is perhaps half the size of the largest (Urogale). The foramen of Ptilocercus is no larger than that of Dendrogale.

In all tupaioids the posterior carotid foramen is located in the posteromedial angle of the bulla (fig. IV-3).

(2) Anterior Carotid Foramen

An alicochlear commissure is found in young stages of _T. glis_, and hence a foramen caroticum primitivum of the usual type is found (fig. IV-18).

Because of the unique way in which the piriform fenestra is covered over by the superior part of the entotympanic, the site of the anterior carotid foramen is not evident without dissection of the roof of the tympanic cavity. As may be seen in fig. IV-4, the promontorial artery passes through the wide interval between the epitympanic wings of the sphenoid and petrosal (the original piriform fenestra or 'foramen lacerum medium' of LE GROS CLARK 1925) in order to enter the cranial cavity.

4.4.3 NERVES

The major nerves traversing the tympanic cavity are illustrated in fig. IV-6.

(1) Facial (VII) Nerve

This nerve shows no peculiarities in its route. In the younger specimens, the facial passes from the cavum supracochleare into the tympanic cavity just in front of the fenestra vestibuli. A well-defined cartilaginous sulcus conducts it to the root of Reichert's cartilage, where it leaves the region of the tympanic cavity. In the older specimens, the nerve is enclosed in a bony tube and the stylomastoid foramen is complete. The stapedius muscle passes beneath the facial in close relation to its sulcus (fig. IV-21) in young stages, but in the adult both have separate bony canals (fig. IV-41). HINCHCLIFFE and PYE (1969:280), however, assert that they share a common canal.

(2) Chorda Tympani

The chorda tympani passes into the tympanic cavity through its own foramen (fig. IV-5) in the adult. It travels around the malleus, then passes out of the middle ear through the Glaserian fissure. In the younger specimens it is closely associated with the proximal part of Meckel's cartilage.

There is no element of Spence.

(3) Internal Carotid Nerve and Deep Petrosal

The internal carotid nerve is quite large. It arises, as usual, from the cranial cervical ganglion and penetrates the posterior carotid foramen in company with the internal carotid artery.

The nerve divides within the carotid canal into medial and lateral branches. These branches pass into the tympanic cavity, in company with the minute inferior tympanic artery, through a small foramen in the yoke formed by the promontorial and stapedial canals. The lateral branch, after receiving a small communicating branch from the tympanic nerve, swings upwards on the lateral face of the promontory. The medial branch travels anteriorly in association with the promontorial artery, but on the outside of its canal. The lateral branch sends out small rami to the tympanic plexus, then rejoins the medial branch lateral to the point where the promontorial artery enters the hind end of the anterior septum. The reconstituted nerve then passes through a foramen in the superior part of the entotympanic, and, as the deep petrosal nerve, follows the greater petrosal to the tympanic aperture of the pterygoid canal within the roof of the tympanic cavity.

(4) Greater Petrosal

The greater petrosal arises from the geniculate ganglion and passes across the cerebral surface of the pars cochlearis. It meets the deep petrosal within the roof of the tympanic cavity beneath the large dehiscence representing the original piriform fenestra (fig. IV-4).

(5) Nerves of the Pterygoid Canal

The route of the nerves of the pterygoid canal (the deep and greater petrosal) cannot be seen from within the tympanic cavity because they travel between the superior part of the entotympanic and the epitympanic wing of the sphenoid. The tympanic aperture of the vidian canal is illustrated in fig. IV-4.

(6) Auricular Ramus of the Vagus

The auricular ramus does not pass through the posterior end of the tympanic cavity. Instead, it circles the posterior part of the bulla (here formed by the original CTPP), then travels into the (extratympanic) stapedius fossa to meet the facial as the latter emerges from the stylomastoid foramen.

(7) Tympanic Nerve and Lesser Petrosal

The stem of the tympanic nerve arises from the glossopharyngeal as usual and travels in close association with the auricular ramus of the vagus in all sectioned specimens. It quickly divides into two branches, both of which are small. One branch follows the internal carotid nerve into the carotid canal and either joins the latter or follows it coaxially to the tympanic plexus. The other branch continues to associate with the auricular ramus of the vagus for a short distance further, then swings anteriorly and broaches the posterior end of the bulla through a foramen located at the original site of the CTPP-entotympanic suture or commissure (figs. IV-5, IV-37). The further relations of this branch are as follows: across the roof of D_3, around the lateral margin of the apertura fossulae fenestrae cochleae, over the stapedial canal and then along the lateral surface of the promontory. As it travels along the promontory it rises towards the roof of the tympanic cavity and enters the tympanic plexus.

The lesser petrosal, the anterior prolongation of the tympanic nerve, emerges from the tympanic plexus and strikes anterolaterally across the roof of the tympanic cavity. It enters a canal in the tegmen tympani just in advance of the foramen for the ramus superior of the stapedial artery. This canal opens into the narrow interval between the appressed parts of the entotympanic and the sphenoid. The nerve travels within the fibrous tissue filling this interval to the otic ganglion at the mouth of the foramen ovale.

Two important relations of the lesser petrosal may be emphasized here. First, the nerve travels in close association with the ramus inferior of the stapedial. This is a common relation in lipotyphlans and further substantiates the identity of this artery. Secondly, the lesser petrosal, like the ramus inferior, travels within the roof of the tympanic cavity. This happens because the entotympanic grows beneath the well-developed epitympanic wing of the sphenoid and covers over the path of the nerve.

SABAN (1963:170, fig. 17B) illustrates a canal for the tympanic nerve on the lip of the posterior carotid foramen. This canal, however, receives only the communicating branch of the nerve. The major part of the tympanic nerve passes into the tympanic cavity through a separate foramen, as noted above.

4.5 SUMMARY OF PRINCIPAL FINDINGS

(1) The fibrous membrane of the tympanic cavity forms the primordial ventral wall of the middle ear, as in other mammals investigated here. However, unlike the tympanic processes of the constant basicranial bones, the entotympanic of *T. glis* actually grows within the membrane itself. The entotympanic functionally replaces the fibrous membrane during ontogeny.

(2) The bony ventral wall is formed by a greatly-inflated (?rostral) entotympanic and a small caudal tympanic process of the petrosal (CTPP). The entotympanic arises in direct continuity with the cartilage of the auditory tube, and the two can be separated only after the completion of entotympanic ossification. The entotympanic has its own centre, but the CTPP ossifies from the pars canalicularis. Reichert's cartilage makes no contribution to the entotympanic. The rostral tympanic process of the petrosal (RTPP)

is either absent or reduced to a small ridge which supports the entotympanic bulla.

(3) The ectotympanic retains the form of a thin anulus and is composed of 'intermediate bone' in the adult. The apex of the posterior crus fuses with the squamosal; the bone is otherwise freely suspended within the entotympanic bulla.

(4) There is never a particularly intimate association between the entotympanic and the ectotympanic. The former simply grows around the latter, always within the fibrous membrane. There is no intermediate stage of edge-to-edge articulation, as there is in lemurs, and sutural tissues are entirely deficient.

(5) The 'anulus membrane' which supposedly connects the ectotympanic to the inner surface of the bulla is merely part of the membranous meatus. As in lemurs, there is a linea semicircularis.

(6) In Tupaiinae, the entotympanic bulla is ringed by small cristae derived from the sphenoid, squamosal and occipital in the adult stage; however, none take part in the construction of the bulla *per se*. In Ptilocercinae, on the other hand, the alisphenoid sends out a very large tympanic process.

(7) The construction of the dorsal wall is curious. The epitympanic wing of the sphenoid is well-developed. However, it is almost completely occluded by the superior part of the entotympanic, which grows beneath the sphenoidal wing and forms a 'second' roof for the anterior part of tympanic cavity. A small epitympanic wing

of the petrosal is also covered by the entotympanic. The tegmen tympani is moderately large, but the squamosal forms no significant part of the roof of the middle ear.

(8) The original piriform fenestra, which lies between the petrosal and the sphenoid as in other mammals, is never closed over through the approximation of these two bones. However, the fenestra is nonetheless entirely hidden from view because of the growth of the entotympanic beneath the epitympanic wing of the sphenoid and the adjacent part of the petrosal.

(9) Pneumatization results in a large hypotympanic sinus, but other cavities are small. Although the major septa of T. glis are superficially similar to those of L. catta, they arise from the entotympanic rather than the petrosal.

(10) The tensor tympani is absent in the available specimens, although others have claimed that the muscle is present in Tupaia. Contrary to the statements of most authors, the ramus inferior of the stapedial artery persists into the adult stage of T. glis. The origin of the stapedius muscle is extratympanic. Routes of the nerves selected for study are typical.

CHAPTER FIVE

MACROSCELIDEA

METHOD OF DESCRIPTION

5.1 VENTRAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

- 5.1.1 Fibrous Membrane of the Tympanic Cavity
- 5.1.2 Cartilage of the Auditory Tube
- 5.1.3 Rostral Entotympanic
- 5.1.4 Caudal Entotympanic
- 5.1.5 Tympanic Processes of the Petrosal
- 5.1.6 Ectotympanic
- 5.1.7 Relationship of the Ectotympanic and Caudal Entotympanic
- 5.1.8 Tympanic Process of the Alisphenoid
- 5.1.9 Tympanic Process of the Basisphenoid
- 5.1.10 Entoglenoid Process of the Squamosal

5.2 DORSAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

- 5.2.1 Tegmen Tympani, Epitympanic Wing of the Petrosal and Reichert's Cartilage
- 5.2.2 Epitympanic Wing of the Sphenoid
- 5.2.3 Epitympanic Wing of the Squamosal

5.3 PRINCIPAL SPACES AND SEPTA OF THE MIDDLE EAR

- 5.3.1 Principal Spaces
- 5.3.2 Principal Septa

5.4 MUSCLES, ARTERIES AND NERVES OF THE MIDDLE EAR

- 5.4.1 Ossicular Muscles
- 5.4.2 Arteries
- 5.4.3 Nerves

5.5 SUMMARY OF PRINCIPAL FINDINGS

5.1 VENTRAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

Macroscelideans are remarkable for the number of separate tympanic processes which compose the ventral wall. In addition to the gonial and element of Spence (which cannot be regarded as true tympanic processes), there are rostral and caudal processes of the petrosal, rostral and caudal entotympanics, and contributions by the ectotympanic, alisphenoid, basisphenoid, pterygoid and squamosal.

Another remarkable feature is the development of the entotympanics. According to the interpretation presented here, the rostral entotympanic develops from a cartilaginous rudiment, but the caudal entotympanic arises as a membrane bone. The rostral entotympanic does not ossify, at least according to available evidence. The caudal entotympanic develops a large mass of what appears to be secondary cartilage along its ventral margin. This tissue may convert directly into bone without any intervening phase of endochondral replacement.

5.1.1 FIBROUS MEMBRANE OF THE TYMPANIC CAVITY

5.1.1.1 Structure, Relations and Development

The fibrous membrane of the tympanic cavity was described by VAN DER KLAAUW (1929:526) under the term "plate of more dense connective tissue in the 'ventral' wall of the tympanic cavity".

In the younger fetus (MPIH 311/E1) the fibrous membrane is well-defined only where it covers the posterior part of the tympanic cavity (fig. V-14). The membrane is attenuated anteriorly, although it can be traced as far as the tympanic aperture of the auditory

Table 5-1

MACROSCELIDEA

SPECIMENS	No.	CRL[1]	HL[2]	ST[3]	PS[4]	STAINS
MACROSCELIDINAE						
Elephantulus fuscipes						
I. Fetus	MPIH 311/E1	31	20	10	cross	Azan, Cresyl Violet
II. Fetus	MPIH 305/E	43	24	10	cross	Azan, Cresyl Violet, PAS-AB

[1] Crown-rump length (in mm)

[2] Head length (in mm)

[3] Section thickness (in mμ)

[4] Plane of sectioning

NOTES ON SPECIMENS

The two fetuses of *Elephantulus fuscipes* were collected from pregnant females trapped in present-day Zaïre by members of the Max-Planck-Institut für Hirnforschung (STEPHAN 1958).

Most sections had been previously stained with Azan and Cresyl Violet, but a few unstained sections of the older fetus (MPIH 305E) were still available at the time of study. These were treated with periodic acid-Schiff reagent and counter-stained with Alcian Blue (denoted as PAS-AB in the table).

Dr. W.B. SPATZ (Neurobiologische Abteilung, MPIH) permitted me to study his personal collection of macerated adult skulls of *Elephantulus rozeti*.

The right auditory region of MPIH 311/E1 was reconstructed from serial sections according to the graphical point-plot method (fig. V-1). Unfortunately, MPIH 305/E had been badly damaged during the original processing procedure and the sections containing the posterior part of the auditory region could not be adequately studied or reconstructed.

tube (fig. V-8). It is also insubstantial lateral to the position of the ectotympanic, and makes only a weak connexion with the periosteum of the auricular cartilage. Medially, it is continuous with the fascial lining of the central system.

Posteriorly, the fibrous membrane leaves Reichert's cartilage and swings inwards to attach to the medial side of the extraordinarily deep fossa for the stapedius muscle (fig. V-14a,b). Accordingly, the muscle must pass through the fibrous membrane to reach the stapes, and its origin is excluded from the presumptive tympanic cavity (cf. *T. glis*, fig. IV-22).

On the other hand, the fibrous membrane clearly invests the periosteum of the ectotympanic (fig. V-11), which is important to an understanding of the development of the ectotympanic-caudal entotympanic relationship (see 5.1.7).

5.1.1.2 Fibrous Membrane and Structures in the Ventral Wall

VAN DER KLAAUW (1929:526) notes that the fibrous membrane forms the periosteum/perichondrium of the RTPP, rostral and caudal entotympanics in older macroscelidean fetuses. It is also his opinion that the fibrous membrane directly gives rise to the caudal entotympanic (1929:534).

In MPIH 311/E1 the entotympanics and the RTPP have not yet formed. However, the posterior spur of the cartilage of the tube (figs. V-1, V-11) is embedded within the fibrous membrane.

In the older fetus (MPIH 305/E) the fibrous membrane cannot be distinguished from the periosteum/perichondrium of the entotympanics (fig. V-21). VAN DER KLAAUW's theory regarding the origin of the material of the entotympanic will be discussed further in section 5.1.4.

5.1.2 CARTILAGE OF THE AUDITORY TUBE

5.1.2.1 Structure, Relations and Development in *Elephantulus fuscipes*

The cartilage of the tube and the rostral entotympanic fuse together in macroscelideans at an early stage of development, although it is quite definite that they chondrify separately (see VAN DER KLAAUW 1929; ROUX 1947). In the younger fetus (MPIH 311/E1) the cartilage of the tube is present, but the rostral entotympanic has not yet formed (see 5.1.3). In the older fetus (MPIH 305/E) both elements are present and united to one another by a fibrous transitional zone.

The cartilage of the tube in young stages of *Elephantulus fuscipes* does not differ significantly from that of the macroscelidean fetuses described in exhaustive detail by VAN DER KLAAUW (1929).

E. fuscipes MPIH 311/E1

Simplifying VAN DER KLAAUW's terminology somewhat, the cartilage of the tube in the younger fetus can be divided into anterior ("pharyngeal") and posterior ("tympanic") sections (fig. V-1). The anterior section consists of that part of the cartilage of the tube which actually encloses the auditory tube. The posterior section is the caudal prolongation of the tubal cartilage beyond the tympanic aperture of the auditory tube (figs. V-6 to V-11).

The auditory tube is oriented in the transverse plane, and thus both the pharyngeal and tympanic apertures of the tube are simultaneously present in most cross-sections (fig. V-8). As usual, the anterior margin of the cartilage of the tube is reflected ventrally and forms a deep trough for the auditory tube (fig. V-1).

In cross-sections, the anterior section appears to consist of dorsal and ventral plates. The ventral plate, which is the reflected anterior margin, ends at the tympanic aperture of the auditory tube (fig. V-8). It has a close association with the stylohyal-ceratohyal articulation, which is accommodated in a slight depression in the ventral plate (fig. V-7). However, it should be noted that the visceral skeleton is not fused to the tubal cartilage.

As may be seen in the reconstruction (fig. V-1), the posterior part of the cartilage of the tube contracts into a narrow spur which extends well beyond the level of the tympanic aperture of the auditory tube. It terminates within the fibrous membrane parallel to the anterior pole of the promontory (fig. V-11).

E. fuscipes MPIH 305/E

In the older fetus conditions are quite similar except for the larger size and better definition of the tubal cartilage. Both entotympanics are present in this specimen, and the cartilage of the tube is closely associated with each.

The anterior extremity of the caudal entotympanic abuts the entire lateral edge of the tubal cartilage (figs. V-17, V-18). However, the two are separated by a thin layer of connective tissue and cannot be considered as fused.

The caudal spur of the posterior section of the cartilage of the tube is well defined until the level of the basioccipital-basisphenoidal synchondrosis. Here it becomes very diffuse and its perichondrium loses its sharp outline. A few sections posterior to this, well defined cartilage again appears, although the cartilage is histologically different from that seen more anteriorly (cf. V-21a,b). Evidently, this diffuse area represents the transitional zone between the cartilage of the tube and the rostral entotympanic.

5.1.2.2 Comparisons

There is some variation in the size and proportions of the tubal cartilage in the macroscelideans studied by VAN DER KLAAUW (see fig. V-5). However, in all general features there is close agreement among species, and *E. fuscipes* displays no significant differences.

The transitional zone between the cartilage of the tube and the rostral entotympanic found in MPIH 305/E was also seen by VAN DER KLAAUW in his specimen III. In his older material this zone was apparently absent, although a structural division between the two elements could still be made. The disappearance of the transitional zone is probably correlated with increasing age.

ROUX (1947) found that the cartilage of the tube and a small rostral entotympanic were separate in a 30 mm CRL fetus of *E. myurus*.[1]

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[1] The *E. myurus jamesoni* of ROUX (1947) is the *E. rupestris jamesoni* of ELLERMAN, MORRISON-SCOTT and HAYMAN (1953).

By the 34 mm CRL stage, the two were completely fused.

It is convenient to discuss at this point the "small separate mass of cartilage" found by VAN DER KLAAUW (1929:529-531) near the posterior end of the rostral entotympanic in his five older specimens. Curiously, VAN DER KLAAUW did not assign a value to this cartilage, although he obviously considered it to be independent of both entotympanics and the tubal cartilage.

No such cartilage exists in either of my specimens. There is a certain correspondence between his text-fig. 14 (1929:520) and my fig. V-18, but the structure in the dorsomedial wall in my illustration is unquestionably the posterior spur of the cartilage of the tube in MPIH 305/E. It seems very doubtful that VAN DER KLAAUW would have confused the anterior basicapsular commissure or its degenerating remnant (which lies in the same area) with this separate cartilage; accordingly, its origin and nature must remain enigmatic.

The chief difference from T. glis (see 4.1.3) is that the cartilage of the tube can be distinguished from the rostral entotympanic even after fusion.

5.1.3 ROSTRAL ENTOTYMPANIC

5.1.3.1 Structure, Relations and Development in Elephantulus fuscipes

The existence of a separate rostral entotympanic in macroscelideans was unknown until VAN DER KLAAUW's (1929) study. References to 'the entotympanic' in the earlier literature (e.g., VAN KAMPEN 1905; CARLSSON 1909) invariably apply to the caudal entotympanic alone.

The rostral entotympanic of Elephantulus fuscipes is much like that of other macroscelideans, except for its relatively small size. Conditions in MPIH 311/E1 suggest that the rostral entotympanic is still absent at the 31 mm CRL stage. This is surprising, for VAN DER KLAAUW found it in his specimen II (28 mm CRL); as noted in fig. V-5, specimen II is probably E. rozeti, not Macroscelides sp. Also, ROUX (1947) described a rostral entotympanic in a 30 mm CRL specimen of E. myurus. However, fetal measurements are at best an imprecise guide, especially when different species are being compared.

In the older fetus (MPIH 305E), the rostral entotympanic extends from the transitional zone behind the posterior spur of the cartilage of the tube to the anterior end of the RTPP, where it abruptly terminates (figs. V-19, V-20, V-21b,c). Compared to the tissue of the cartilage of the tube, the cartilage of the rostral entotympanic appears to be less organized. The intercellular matrix is very liberally supplied with thick fibers, and the lacunae are quite angular and unevenly distributed. It shows none of the regressive changes which accompany endochondral ossification.

Anteriorly, the rostral entotympanic is separated from the dorsal margin of the caudal entotympanic by a transitional zone similar to that separating the rostral entotympanic from the cartilage of the tube. This tissue gradually thins posteriorly, and the terminal part of the rostral entotympanic appears to be fused to the caudal entotympanic (fig. 21b,c).

Because VAN DER KLAAUW (1929) claims that the rostral entotympanic forms part or all of the tympanic process of the basisphenoid of other authors, discussion of the later fate of the rostral entotympanic will be reserved for section 5.1.9.

5.1.3.2 Comparisons

VAN DER KLAAUW found some variation in the degree to which the rostral entotympanic resembled hyalin cartilage, the resemblance being stronger in younger specimens. Bands of connective tissue, evidently large bundles of collagen fibers, are described as perforating the substance of the rostral entotympanic in specimens V and VI. This suggests a histological picture similar to that seen in MPIH 305/E.

VAN DER KLAAUW also found continuity of the two entotympanics in some specimens. It is evident from his descriptions and illustrations that in other specimens the two elements were separated by a few layers of connective tissue at most.

5.1.4 CAUDAL ENTOTYMPANIC

5.1.4.1 Introduction

The ontogenetic independence of the caudal entotympanic was first demonstrated by PARKER (1886). VAN DER KLAAUW (1929) made a detailed investigation of this element in the course of his examination of bullar ontogeny in fetal elephant shrews. ROUX (1947) studied no fewer than thirteen prenatal stages of Elephantulus myurus, but found no sign of the caudal entotympanic in any of them. He concluded that the caudal entotympanic had undergone fusion primordiale with the CTPP, but this view is probably erroneous (see below).

The caudal entotympanic of the adult has been described, in greater or lesser degrees of detail and accuracy, by VAN KAMPEN (1905), CARLSSON (1909), GREGORY (1910), VAN DER KLAAUW (1931), KEEN and GROBBELAAR (1941), EVANS (1942), and SABAN (1956-57).

5.1.4.2 Structure, Relations and Development in *Elephantulus fuscipes*

There is a component of the medioventral wall of the tympanic cavity in the older fetus (MPIH 305/E) which corresponds in form, location and certain special histological characteristics to the caudal entotympanic of VAN DER KLAAUW (1929). This confirms that a separate caudal entotympanic is present in all macroscelideans including *Elephantulus* (*contra* ROUX 1947).

E. fuscipes MPIH 311/E1

According to VAN DER KLAAUW (1929), the anlage for the caudal entotympanic appears immediately above the ectotympanic and within the fibrous membrane of the tympanic cavity. The anlage is said to be unlike typical cartilage (see 5.1.4.3) and instead consists of large, lightly-staining cells in a thin matrix. Close inspection of the fibrous membrane in MPIH 311/E1 failed to reveal any sign of this tissue (fig. V-11), and thus the anlage of the caudal entotympanic must form later than the 31 mm CRL stage in *E. fuscipes*.

E. fuscipes MPIH 305/E

In the older fetus the caudal entotympanic is very large and forms the greater part of the developing tympanic bulla. Its relations appear to be identical to those found in other macroscelideans (see fig. V-5). Anteriorly, it meets the anterior margin of the cartilage of the tube near the tympanic aperture of the auditory tube (fig. V-17). Dorsomedially, it is in contact with the caudal spur of the cartilage of the tube, the rostral entotympanic (with which it is partially fused), and the RTPP (figs. V-18, V-19, V-20). Ventrally, it adjoins the ectotympanic (fig. V-18, V-19, V-20). Unfortunately, destruction of tissue was too great for a determination of its relationship with the CTPP.

It has the form of a simple plate and does not contribute to the construction of the roof of the tympanic cavity. Nor does it form commissures with the tegmen tympani or (judging from VAN DER KLAAUW's descriptions), the CTPP. VAN DER KLAAUW (1929) also notes that there is no primary association with Reichert's cartilage, which is a similarity to Tupaia and a number of other mammals with entotympanics.

The caudal entotympanic possesses a unique histological structure. The ventral moiety consists of trabeculae of young fibrous bone, while the dorsal moiety is composed of a cartilage-like material featuring large, round cells in a thin, poorly-staining matrix (fig. 21a,b,c). There is a continuous gradation between the bony and cartilage-like areas, and they are never separated by periosteal/pericondrial tissues. There is no sign of the regressive changes which accompany the calcification, degeneration and removal of cartilage. VAN DER KLAAUW (1929) hypothesized that a metaplastic event occurs in the formation of the caudal entotympanic whereby cartilage transforms directly into bone. This theory demands separate treatment and will be discussed further in section 5.1.4.3.

E. rozeti adults

The caudal entotympanic is entirely bony and forms the medial part of the compound bulla (fig. V-3). It is completely fused with the expanded ectotympanic and the suture which originally lay between them is obliterated.

The caudal entotympanic does not fuse with either the RTPP or the CTPP. Instead, it forms small articular surfaces which rest on similar flanges on the petrosal plate (fig. V-2).

5.1.4.3 Histology and Histogenesis of the Caudal Entotympanic

(1) Van Der Klaauw's (1929) Observations on Fetal Macroscelideans

According to VAN DER KLAAUW(1929), the anlage of the caudal entotympanic appears within the fibrous membrane of the tympanic cavity and initially consists of small islets of large, round, weakly-staining cells which differ from those in the surrounding mesenchyma. A thin matrix is elaborated around these cells, giving the tissue a highly-cellular, cartilage-like appearance (Zellenknorpel of VAN DER KLAAUW). These cells are illustrated as chondrocytes in his semi-schematic text-figures.

However, instead of continuing to develop as typical cartilage, spicules which stain like bone matrix begin to appear around the cells of the caudal entotympanic rudiment. These spicules join to form trabeculae of young woven bone; coincident with this development, definite bone cells begin to appear. As the caudal entotympanic continues to develop, the cartilage-like material is gradually transformed into bone tissue of normal aspect.

Now, the significant matter here is that VAN DER KLAAUW argued for direct, metaplastic transformation of cartilage into bone. None of his specimens showed any signs of regressive changes in the cartilage-like material, and thus endochondral replacement did not occur. Further, in every case in which both the cartilage-like material and bone tissue were present in the rudiment, the one tissue graded insensibly into the other.

E. fuscipes MPIH 305/E was carefully studied in order to determine whether VAN DER KLAAUW's descriptions could be supported. Although he (1929:542) specifically disagreed with the interpretation that the cartilage-like material was secondary cartilage, I believe that this constitutes the best explanation. In my view, the macroscelidean caudal entotympanic has to be regarded as a member of the class of membrane bones which develop secondary cartilage as a normal feature of their ontogeny (e.g., pterygoid, squamosal, palatine). However, the secondary cartilage of the caudal entotympanic seems to be of the sort described by MOSS (1958) as 'intermediate', i.e., a form of secondary cartilage which does in fact transform directly into bone.

(2) Observations on E. fuscipes MPIH 305/E

Only the older fetus shows evidence of the caudal entotympanic, and in this specimen the element is advanced well beyond the anlage stage. Unfortunately, the style of processing affected the histological characteristics of the tissues to some degree. The staining with Azan and Cresyl Violet was adequate, but the PAS-AB reaction was rather poor. Accordingly, little emphasis will be placed on the visualizations gained with the latter method.

(i) Azan

The matrix of the dorsal moiety stains a pallid shade of blue (fig. 21b). Coloration varies along a dorsoventral gradient, the matrix of the upper part of the moiety being virtually colorless.

Cells in the central region of the moiety are large, but their cytoplasm stains weakly and lacunae are poorly-marked. Cells of this form grade into darker-staining ones on all sides.

The matrix of the ventral moiety is continuous with that of the dorsal, but it is much better defined. It grades from deep blue above to deep blue with reddish nuances below. The cellular constituents appear to be normally-shaped osteoblasts and osteocytes, and are intensely stained. Osteoblasts are very sparsely distributed.

(ii) Periodic Acid-Schiff with Alcian Blue

The dorsal moiety colors etiolated shades of blue to blue-green (fig. 21a), indicating that very little Alcian Blue was picked up by the matrix in this area. Cytoplasmic glycogen droplets are virtually absent, whereas they are common and prominent in the cartilage of the tube, rostral entotympanic, and other cartilaginous tissues.

Definition of the matrix increases as the ventral moiety is approached. Here, the intercellular substance gives a weak but visible

PAS-positive reaction, and coloration varies from pale bluish-red to pale magenta.

(iii) Cresyl Violet

Cresyl Violet is a basic dye and ordinarily colors cartilage matrix varying shades of reddish-purple to dark purple, depending on the degree of calcification. Even very young cartilage matrix picks up a small amount of dye. Bone matrix, on the other hand, colors a pale to extremely pale blue.

The matrix of the ventral moiety is a very pale blue, as would be expected for young bone (fig. 21c; cf. alisphenoid in same figure). The rostral entotympanic colors a pale purple. Both contrast with the dorsal moiety of the caudal entotympanic, the intercellular matrix of which is nearly devoid of color.

This is curious, for the matrix of young cartilage is basophilic because of the acidic sulphate groups in chondromucoprotein, the principal constitutent of cartilage ground substance (BLOOM and FAWCETT 1968:214). This lack of basophilia with Cresyl Violet confirms the findings with PAS-AB, where the Alcian Blue failed to stain the matrix of the dorsal moiety to any significant degree.

As with the other methods, no calcified cartilage was visualized.

In summary, there is not much to suggest that the material of the dorsal moiety is true cartilage. The cells are large, but the absence of significant staining with either Alcian Blue or Cresyl Violet suggests that the matrix is not that of typical primary cartilage.

On the other hand, all histological signs indicate that the ventral moiety is composed of bone tissue of normal aspect.

(3) Comparisons to Secondary Cartilage

If the material is not typical cartilage, it may be a form of secondary cartilage.

In MPIH 305/E the only areas still showing secondary cartilage were the pterygoid hamulus and the mandible. In both cases lacunae were well-developed, the matrix was quite basophilic, and cells displayed regressive changes. However, this secondary cartilage is the 'definitive' type of MOSS (1958) and typically undergoes endochondral replacement.

Since the caudal entotympanic is a bullar component, a comparison to the secondary cartilage in the petrosal plate of Microcebus murinus MPIH 1964/42 (see 2.1.3.2 and fig. II-12) is in order. There were several similarities, including the poor degree of definition of most lacunae, general thinness of matrix, and areas of continuity between secondary cartilage and bone matrix. However, there were also signs of regressive changes in the secondary cartilage, and for this reason it was classified as the 'definitive' type.

MOSS (1958:152) describes 'intermediate' secondary cartilage as being of a lower order of differentiation than the 'definitive' type. Although it has so far been described only in sutural tissues, it is possible that it can be evoked elsewhere. In any event, the strongest similarities appear to lie between this form of secondary cartilage and the material composing the dorsal moiety of the caudal entotympanic (cf. 'intermediate' secondary cartilage in ectotympanic-petrosal plate suture of Galago senegalensis MPIH 1967/117 (fig. III-9) and caudal entotympanic of E. fuscipes MPIH 305/E (fig. V-21b)).

An important consideration for this problem is the relation of blood supply to the production of secondary cartilage. Much greater armounts of secondary cartilage appear at fracture sites in cranial bones when blood supply is reduced (PRITCHARD, SCOTT and GIRGIS 1956:83). It has also been argued that cells of the developing mandible which may differentiate as either cartilage or bone will become chondrogenic if blood supply is lowered, but osteogenic if the supply is adequate (see HALL 1968).

Although VAN DER KLAAUW (1929) implies that blood vessels penetrate the dorsal moiety extensively, MPIH 305/E does not confirm entirely to what would be expected from VAN DER KLAAUW's descriptions. The greatest concentration of blood vessels anywhere in the caudal entotympanic of this specimen occurs precisely where bone changes over to secondary cartilage (fig. V-21). One might speculate that blood vessels carry in cells capable of becoming osteoblasts, which then begin to form bone matrix. Or, they may produce some effect on the cells composing the secondary cartilage, causing them to differentiate (or modulate) into osteoblasts.

5.1.4.4 Conclusions

The best interim analysis, in the absence of other material, is that the caudal entotympanic develops as a membrane bone. Like some other membrane bones, it develops areas of secondary cartilage.

Secondary cartilage probably appears in the fetal mammal for a variety of reasons, depending on local tissue conditions (see references in section 2.1.3.3). In the absence of any obvious influence of pressure transfer or stress, it may be concluded that the production of secondary cartilage in the caudal entotympanic of elephant shrews is probably correlated with rapid growth combined with an inadequate blood supply to part of the rudiment.

The likely importance of rapid growth may be illustrated by the fact that the caudal entotympanic is not even present in anlage at the 31 mm CRL stage (MPIH 311/E1), but constitutes most of the medioventral wall of the tympanic cavity by the 43 mm CRL stage (MPIH 305/E).

An admitted peculiarity of this secondary cartilage is its apparent direct transofrmation into bone. So far, such transformation is best known in sutural tissues, although the reality of the metaplastic transformation of different types of specialized connective tissues into bone can no longer be doubted (see review in HAINES and MOHUIDDIN 1968).

Thus, VAN DER KLAAUW's (1929) advocacy of a metaplastic event in the histogenesis of the caudal entotympanic is supportable. However, rather than contribute to the complicated terminology which already exists for metaplastic tissues, I prefer to regard the material which forms part of the rudiment of the caudal entotympanic as a type of secondary cartilage.

In favor of the view that the caudal entotympanic is a membrane bone is VAN DER KLAAUW's (1929) description of its anlage, which conforms reasonably well to the early stages of intramembranous ossification even though the cellular constituents have an unusual form. The absence of any detectable endochondral replacement of the primordium reinforces this. That the caudal entotympanic should form in membrane rather than in cartilage is not unique; while the entotympanic is usually preformed in cartilage, it is known to arise intramembranously in at least one other form (the three-toed sloth *Bradypus*; SCHNEIDER 1955).

The development of the macroscelidean caudal entotympanic provides secure evidence that the fibrous membrane of the tympanic cavity has skeletogenic potential (see also 4.1.3). This matter will be discussed further in section 8.5.2.

Needless to say, there is no occasion to consider the possibility that the secondary cartilage of the caudal entotympanic represents a phylogenetically independent element that has undergone *fusion primordiale*, since virtually every bone in the posterior part of the mammalian basicranium is already represented in the macroscelidean bulla.

Equally, ROUX' (1947) contention that the caudal entotympanic undergoes *fusion primordiale* with the CTPP in *Elephantulus myurus* is undoubtedly mistaken. The point cannot be definitely proven here because I have investigated a different species of *Elephantulus*. However, the following points demonstrate that ROUX' argument is highly unlikely:

(1) ROUX (1947:258-259) advanced as his major ground for invoking fusion primordiale the fact that the caudal entotympanic was still absent in his oldest (34 mm CRL) stage of E. myurus, while the rostral entotympanic was present in the 30 mm CRL stage. The significance of this relates to VAN DER KLAAUW's (1922) theory that the 'caudal chamber' of the tympanic cavity (i.e., diverticulum D_3 or the saccus posterior) is older than the ventral wall between the ectotympanic and the petrosal. VAN DER KLAAUW (1929) regarded the fact that the anlage of the caudal entotympanic appeared before the rostral entotympanic in his macroscelidean material as a further demonstration of his theory. However, the relative order of appearance of elements is no sure guide to their phylogenetic antiquity because of the possibility of heterochrony (DE BEER 1958).

(2) Since the CTPP was present in his older specimens, ROUX (1947) theorized that fusion primordiale had occurred and that the CTPP was composed of both caudal entotympanic and petrosal material. He attempted to substantiate his argument by comparing E. myurus to the bat Rousettus amplexicaudatus, but in the latter the caudal entotympanic forms separately and secondarily fuses to the CTPP (VAN DER KLAAUW 1922). Fusion secondaire also occurs in T. glis (see 4.1.3), but the CTPP and entotympanic are easily separated in the early stages of bullar ontogeny.

(3) In the adult E. rozeti the CTPP is separated from the caudal entotympanic by a complete suture (figs. V-2, V-3), which surely indicates that they form separately. The situation is the same in

other macroscelideans (VAN KAMPEN 1905), and there is no reason to suppose that *E. myurus* differs in this respect.

Accordingly, the likeliest explanation is simply that the caudal entotympanic forms later than the 34 mm CRL stage of *E. myurus*.

5.1.5 TYMPANIC PROCESSES OF THE PETROSAL

5.1.5.1 Caudal Tympanic Process of the Petrosal

Since the posterior end of the auditory capsule of MPIH 305/E is badly fragmented, the fetal condition of the CTPP must be deduced from MPIH 311/E1.

It is evident from VAN DER KLAAUW's (1929) descriptions that the CTPP is large and well-developed in older fetuses of elephant shrews. However, in MPIH 311/E1 only the medial part of the eventual CTPP is easily discerned. It consists of a lateral prolongation of the processus recessus (or MWF) beneath the apertura fossulae fenestrae cochleae (figs. V-1, V-14a,b,c). The CTPC is entirely cartilaginous at the 31 mm CRL stage and is, as usual, continuous with the rest of the auditory capsule.

The relations of the CTPP in adult *E. rozeti* (see figs. V-2, V-3) can be easily determined because the suture between this process and the caudal entotympanic remains open.

The CTPP is hemispherical in form and concave anteriorly. The leading edge broadly articulates with the rear margin of the caudal entotympanic. The CTPP is continuous with the bone of the auditory dorsally, as would be expected on the basis of fetal conditions.

The original boundary between the RTPP and CTPP probably lies at or near the site of the posterior carotid foramen. In the adult the two processes are, of course, continuous and form a single petrosal plate.

In the adult stage, the lateral wall of the CTPP lies against two small foramina and the tympanohyal (fig. V-2, V-3). The anterior of the foramina is unquestionably the foramen stylomastoideum definitivum. The other foramen lies within a short groove and is situated on the medial side of the prominence of the lateral semicircular canal. In life, this foramen evidently contains the stapedius muscle; thus, as in Tupaia (see 4.1.4), this muscle has an extratympanic origin on the sidewall of the skull and its tendon must pass through an aperture in the bulla in order to reach the stapes.

Diverticulum D_3 is relatively more spacious than in the fetus, indicating that the DTPP inflates to a moderate extent during ontogeny. Nothing interrupts the roof of D_3 save for a small prominence which corresponds to the ampullar end of the posterior semicircular canal.

5.1.5.2 Comparisons

The CTPP of MPIH 311/E1 is evidently less developed than in any of VAN DER KLAAUW's (1929) specimens (fig. V-5). Since he did not adequately describe or illustrate the relations of the CTPP to the rest of the auditory capsule, it is sometimes difficult to correlate my observations with his.

He does not mention the processus recessus, although it is evident from his descriptions that it is this structure which gives rise to his 'ventromedial wing' of the CTPP. ROUX (1947:255, fig. 31B) appears to have reached the same conclusion.

It seems clear that VAN DER KLAAUW's 'ventrolateral wing' of the CTPP arises from the massive cartilaginous eminence which forms the lateral margin of the apertura fossulae fenestrae cochleae and the medial wall of the stapedius fossa as well (fig. 14a,b,c). In MPIH 311/E1, however, it is not possible to differentiate this part of the CTPP (posterior and lateral sections of the CTPP of this study; see 1.4.3 and fig. I-2) from the rest of the eminence.

VAN DER KLAAUW (1929) mentions that in some of his specimens the CTPP also arises from a crest on the roof of the tympanic cavity ventromedial to the stapes. Although he does not illustrate this crest, it appears to conform to the most anterior part of the CTPP seen in *Tupaia glis* (fig. IV-21), *Erinaceus europaeus* (fig. VI-15), and tenrecs (fig. VII-16). Unfortunately, this crest could not be securely identified in MPIH 3-1/E1 and the equivalent area in MPIH 305/E is badly disrupted.

ROUX (1947) identifies a CTPP in fetal *E. myurus*.

5.1.5.3 *Rostral Tympanic Process of the Petrosal*

The RTPP is not present in MPIH 311/E1, and description of its form and relations in MPIH 305/E is obviated by tissue damage. However, comparison of VAN DER KLAAUW's (1929) observations with conditions in adult E. rozeti establishes that the process arises intramembranously from the entire length of the ventral surface of the promontory, helps to form part of the epitympanic wing of the petrosal, and migrates medially as a result of pneumatization (as in strepsirhines).

In the adult, the RTPP (like the CTPP) is separated from the caudal entotympanic by a complete suture, and displays a broad articular flange for the latter element (fig. V-2).

VAN DER KLAAUW (1929:499) mentions that in his youngest specimen there was a "short, small, free piece of hyalin cartilage" near the position of the presumptive posterior carotid foramen. He regarded this piece of cartilage as possibly the rudiment of the RTPP (fig. V-5).

What is meant by "free" in this context cannot be established from VAN DER KLAAUW's descriptions. The necessary implication is that the RTPP forms independently and then fuses with the promontory, but this conflicts with all of his other analyses.

MPIH 311/E1 shows a degree of development of the auditory region which is roughly equivalent to VAN DER KLAAUW's specimen I. There is a local thickening of the fibrous membrane of the tympanic cavity in the place specified by VAN DER KLAAUW, i.e., where the internal carotid passes into the middle ear (fig. V-12). No cartilage cells were present in this thickening, which represents no more than the wall of the membranous carotid foramen.

5.1.6 ECTOTYMPANIC

5.1.6.1 Structure, Relations and Development

The ectotympanic expands laterally during ontogeny and forms a long, semitubular external acoustic canal in the adult (fig. V-3).

The ectotympanic is initially anular in form, but presents some differences from young strepsirhines and tupaioids. It is U-shaped rather than C-shaped (fig. V-1) and the tympanic notch faces posteriorly rather than dorsally. This positioning is retained throughout ontogeny.

In MPIH 311/E1 the ectotympanic is present and free of all other skeletal elements. The sulcus for the tympanic membrane is hardly indicated at this stage (fig. V-11). The bone is of fairly even thickness except for the apical region of the anterior crus, which is slightly broadened (fig. V-1).

The older fetus (MPIH 305/E) displays some minor developmental changes. With the exception of the apex of the anterior crus, the lateral margin of the ectotympanic is not significantly expanded. The anterior crus extends laterally beyond the squamosal and thus appears on the exterior wall of the skull (figs. V-17, V-18, V-19, V-20). The ectotympanic is closely associated with or borders on the gonial, tegmen tympani, squamosal, tympanic wing of the alisphenoid, and caudal entotympanic, but is not fused to any of them.

Adult conditions as they appear in E. rozeti are depicted in fig. V-3. The posterior crus is completely fused to the caudal entotympanic, but a suture remains open between the anterior crus and the tympanic process of the alisphenoid. Because of its orientation, the anterior crus curves beneath the tegmen tympani (to which it is lightly fused) and completes the dorsal margin of the external auditory canal. SABAN (1956-57) records that the ectotympanic forms a complete circle, but this is not the case. The apices of the crura are in fact well-separated, and the posterior wall of the external auditory canal is formed by the petrosal.

Not visible in either illustration of the adult is a large, triangular process which arises from the anterior crus. This process is visible, recessed within the external acoustic canal, in undissected bullae. SABAN (1956-57:24, fig. 37) considers it to be the anterior spine, to which the upper part of the pars tensa of the tympanic membrane attaches.

5.1.6.2 Comparisons

The ectotympanic was still nearly anular in form and completely free of the caudal entotympanic in VAN DER KLAAUW's (1929) oldest specimens (fig. V-5). Lateral broadening and synostosis with the caudal entotympanic are thus late ontogenetic developments.

VAN DER KLAAUW did not find any sign of the accessory meatal ossicles described by PETERS (1852). The latter author appears to be the only source who has recorded their presence. These ossicles were not present in MPIH 305/E.

5.1.6.3 Inclination of the Ectotympanic

The sample of elephant shrews is too limited for inferences about the method of ectotympanic rotation. However, the mechanism

Table 5-2

INCLINATION OF THE ECTOTYMPANIC IN YOUNG MACROSCELIDEA

Specimen No.	Angle of Inclination L	Angle of Inclination R	Average Inclination
Elephantulus fuscipes			
MPIH 311/E1	19°	21°	20.0°
MPIH 305/E	26°	25°	25.5°

For computation of angle of inclination, see note accompanying table 2-2.

is probably similar to that seen in lorises (3.1.4.2) since the caudal entotympanic maintains an edge-to-edge articulation with the ectotympanic throughout ontogeny (cf. conditions in T. glis, section 4.1.5.2).

SABAN (1956-57) records a value of 50° for the inclination of the ectotympanic in adult macroscelideans.

5.1.7 RELATIONSHIP OF THE ECTOTYMPANIC AND CAUDAL ENTOTYMPANIC

The caudal entotympanic and ectotympanic are in edge-to-edge articulation throughout bullar ontogeny. Typically, obliteration of the suture lying between them is so complete that the transition from one bone to the other cannot be detected in the adult without references to landmarks like the crista tympanica.

It is possible to detect all five sutural layers of PRITCHARD, SCOTT and GIRGIS (1956) in MPIH 305/E, but the layers are not elaborated to the degree seen in perinatal lorises (see section 3.1.5). The caudal entotympanic forms within an already differentiated fibrous membrane, the fibrous membrane of the tympanic cavity. The fibrous membrane is strongly attached to the ectotympanic (see 5.1.1, fig. V-11), and it provides the uniting layers for the ectotympanic-caudal entotympanic suture in the same way that the ectomeninx does for the bones of the cranial vault (see PRITCHARD, SCOTT and GIRGIS 1956). Both the ectotympanic and caudal entotympanic are provided with complete cambial and capsular layers which are separated by an extremely narrow but well-vascularized middle layer.

The most apparent difference from the ectotympanic-petrosal plate suture of perinatal lorises is the poor development of the middle layer in MPIH 305/E, but PRITCHARD, SCOTT and GIRGIS found equally narrow middle layers in some of the sutures they investigated. There is a clear difference from lemurs (see 2.1.5), in which the middle layer and probably the lateral uniting layer are not developed at all. There is also a clear difference from tree shrews, in which sutural tissues do not form between the ectotympanic and entotympanic at all (see 4.1.6).

The mere presence of all sutural layers does not ensure synostosis; their major function (besides providing flexibility) is to keep advancing bone territories in tandem. In lorises, sutural closure is preceded by the development of 'intermediate' secondary cartilage within the ectotympanic-petrosal plate suture (fig. III-9). However, E. fuscipes MPIH 305/E displayed no sign of this tissue in the part of the ectotympanic-caudal entotympanic suture which could be investigated. Similarly, the suture was still open in VAN DER KLAAUW's (1929) oldest specimens.

Thus, although sutural closure terminates in complete obliteration in macroscelideans, it must occur late in bullar ontogeny (probably well after birth).

5.1.8 TYMPANIC PROCESS OF THE ALISPHENOID

The anterior end of the adult macroscelidean bulla is completed by a true tympanic process of the alisphenoid which articulates with the ectotympanic. This process is large hemispherical in form, and concave posteriorly (fig. V-2). It springs transversely from the body of the alisphenoid, from the gutter for the auditory tube medially to the entoglenoid process of the squamosal laterally.

The tympanic process of the alisphenoid is not represented in MPIH 311/E1, although conditions in the older fetus (MPIH 305/E) suggest that the process initially arises from the slight ridge which follows the sulcus for the ramus inferior artery (fig. V-1).

In MPIH 305/E the tympanic process is well-developed and has assumed a hemispherical form (figs. V-15, V-16). It grows in true dermal bone fashion and shows no sign of secondary cartilage. The process has formed an articulation with the anterior crus of the ectotympanic by this stage, and a complete array of sutural tissues intervene between the two.

5.1.9 TYMPANIC PROCESS OF THE BASISPHENOID

Several authors (e.g., VAN KAMPEN 1905; WEBER 1927-28; WEGNER 1942; SABAN 1956-57) have claimed that there is a tympanic wing of the basisphenoid which participates in the macroscelidean bulla. VAN DER KLAAUW (1929), however, denies a basisphenoidal origin for this process and instead claims that it is formed by an ossified rostral entotympanic.

Investigation of conditions in the two fetuses of *E. fuscipes* and the macerated skulls of adult *E. rozeti* suggests that VAN DER KLAAUW's interpretation is unlikely and that the tympanic process in question is formed not only by the basisphenoid but by the pterygoid as well (at least in *Elephantulus*).

Clarity of discussion will be aided if the structure of the anteromedial portion of the adult bulla is described first. In the macerated adults (fig. V-4) the large, triangular aperture for the auditory tube breaches this portion of the bulla. It is bounded anteriorly by the tympanic wing of the alisphenoid, posteriorly by the caudal entotympanic, and dorsomedially by a low ridge which is continuous with the basisphenoid and medial pterygoid lamina. It is this ridge which VAN DER KLAAUW regards as the bony rostral entotympanic. However, close inspection of this ridge after removal of the tympanic processes of other bones shows that no sutures separate it from the basisphenoid medially or the alisphenoid laterally. It is entirely separate from the caudal entotympanic (fig. V-2).

Of particular interest is the conformation of the tubal aperture itself. Its posterior angle terminates in a long incisure which ends precisely where the petrosal plate begins. The position of this incisure conforms to the position of the small rostral entotympanic found in MPIH 305/E, i.e., directly in front of the RTPP and directly above the anterior part of the caudal entotympanic. These relationships indicate to me that the rostral entotympanic probably occupies this incisure during life, and that it never ossifies. Naturally, it cannot be identified in macerated skulls.

It still remains to determine the identity of the ridge on the dorsomedial margin of the tubal aperture. The two sectioned fetuses are helpful in this regard.

In MPIH 311/E1 the posterior end of the pterygoid bone is not yet fused to the basisphenoid (figs. V-6, V-7, V-8). The pterygoid terminates in a short spit which projects between the basisphenoid and the cartilage of the tube (fig. V-1). A useful landmark is the route of the nerves of the pterygoid canal: at this stage they are not truly enclosed by their own canal, but pass anteriorly between the pterygoid and the basisphenoid. There is no specific crest on the basisphenoid which could be regarded as a tympanic process at this stage.

In MPIH 305/E the posterior end of the pterygoid is completely fused to the basisphenoid and adjacent part of the alisphenoid. However, it is still possible to separate them anatomically by reference to the (now complete) pterygoid canal (figs. V-15, V-16). Material derived from the pterygoid must lie beneath the canal. These figures also establish that the shallow gutter leading up to the tubal foramen, in which the cartilage of the tube is seated, is also derived from the pterygoid bone. Finally, the medial margin of the fused pterygoid-basisphenoid is slightly raised in this area and forms a small ridge (figs. V-15, V-16, V-17). If description is accurate so far, this ridge must be composed of both pterygoidal and basisphenoidal material. The rostral entotympanic lies far behind the transverse level illustrated in fig. V-17, and is thus not in a position to contribute to the ridge.

From these observations I conclude that it is correct to regard the small revetement defining the dorsomedial margin of the tubal foramen in the adult as partly basisphenoidal and partly pterygoidal in origin. Inasmuch as the ridge defines a part of the ventral wall, it is appropriate to call it a 'tympanic process of the basisphenoid' (or better, of both the basisphenoid and pterygoid). It is vestigial compared to the tympanic process of the basisphenoid found in erinaceomorphs, although it is actually better defined than the minute crest found in the same position in soricids (see MCDOWELL 1958).

The identification of a tympanic process of the basisphenoid makes macroscelideans even more exceptional than VAN DER KLAAUW (1929) thought in regard to the number of elements participating in its construction. In closing, it may be noted that VAN DER KLAAUW himself found a small crest on the basisphenoid in one of his specimens, indicating that conditions in Elephantulus are not unique (fig. V-5, specimen III).

5.1.10 ENTOGLENOID PROCESS OF THE SQUAMOSAL

In the adult E. rozeti and other macroscelideans the entoglenoid process is prolonged ventrally and participates in the anterolateral wall of the bulla (fig. V-2). Although external inspection suggests that the entoglenoid process merely overlaps the tympanic process of the alisphenoid, removal of the ectotympanic and caudal entotympanic reveals that the alisphenoid component is deficient laterally and that the entoglenoid indeed forms a part of the bullar wall.

The entoglenoid process also articulates with the anterior crus of the ectotympanic (fig. V-2).

I can confirm ROUX' (1947) observation that the entoglenoid process is of insignificant size even in old fetuses, for it is barely distinguishable from the rest of the glenoid surface in MPIH 305/E (figs. V-16, V-17, V-18).

5.2 DORSAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

The contributions of the various bones making up the roof of the middle ear are illustrated in fig. V-2 (for adult E. rozeti).

The anterior segment of the roof is completed by the epitympanic wing of the sphenoid. SABAN (1956-57:22, fig. 36B) illustrates a suture running through this wing in Macroscelides[1] which divides it into basisphenoidal and alisphenoidal components. However, no suture exists in this position in E. rozeti.

The rest of the roof is formed by the petrosal (tegmen tympani and epitympanic wing of the petrosal), along with a small contribution by the anterior crus of the ectotympanic which forms the dorsal margin of the external acoustic canal.

Neither the entotympanics nor the squamosal appear in the dorsal wall.

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[1] SABAN's figures for Macroscelides do not differ in any significant way from my specimens of Elephantulus rozeti. In his list of specimens two species of Macroscelides are listed, one of which is M. rozeti. THOMAS and SCHWANN (1906) transferred rozeti to their new genus Elephantulus, and references to 'Macroscelides' rozeti are taxonomically inaccurate (see PATTERSON 1965:309). Since one of the significant characters used by THOMAS and SCHWANN was the size of the bulla (Macroscelides, large bullae; Elephantulus, small bullae), it is probable that SABAN has illustrated Elephantulus rozeti rather than a recognized species of Macroscelides. However, the point is not definite and I have not changed the generic name where I cite his illustrations or descriptions.

5.2.1 TEGMEN TYMPANI, EPITYMPANIC WING OF THE PETROSAL, AND REICHERT'S CHARTILAGE

5.2.1.1 Tegmen Tympani

The tegmen tympani is relatively larger in macroscelideans than in such insectivores as *Erinaceus*, although not as large as that of strepsirhines. Further, the petrosal contribution to the roof of the middle ear is substantially increased by an epitympanic wing which is initially separate from the tegmen tympani (fig. V-1). The wing is indivisibly fused with the tegmen tympani in the adult.

E. fuscipes MPIH 311/E1

The tegmen tympani is massive in the younger fetus (fig. V-1). From its origin on the pars canalicularis it strikes anterolaterally to cover the ossicular chain. It displays a shallow but broad fossa on its ventral surface which conforms to the limits of the epitympanic recess of the adult. The tegmen tympani is separated from the epitympanic wing of the sphenoid and the glenoid region of the squamosal by a broad gap, the piriform fenestra. The fenestra is continued posteriorly and separates the developing epitympanic wing of the petrosal from the tegmen tympani *per se*.

The posterior part of the tegmen tympani is deeply grooved by the facial sulcus and displays a capacious fossa incudis. The crista parotica is extremely large and has a prominent posterior continuation (see 5.1.5; fig. 14).

The anterior margin presents a small gutter which accommodates the proximal part of the stapedial artery. At this stage the foramen for the ramus superior has not been incorporated into the tegmen tympani, and the vessel leaves the presumptive tympanic cavity through a membranous foramen in the piriform fenestra (fig. V-1).

The epitympanic wing of the petrosal is represented by a small projection on the anterolateral surface of the promontory. At this stage, the wing is mainly given over to the formation of a shallow fossa for the tensor tympani. Later in ontogeny, it grows anteriorly and laterally, and completely coalesces with the tegmen tympani. The area of the epitympanic wing is also increased by the inflation of the PTPR (see 5.1.5).

E. fuscipes MPIH 305/E

Only the anterior section of the tegmen is sufficiently well preserved for description.

The lateral section of the epitympanic wing of the petrosal and the tegmen tympani have coalesced and form a broad plate which articulates with the epitympanic wing of the sphenoid (figs. V-18, V-19, V-20). As a result, the piriform fenestra is almost completely closed and has been converted into the petrosphenoid suture.

Complete bony canals enclose the ramus inferior and superior and the preserved section of the tegmen tympani is entirely bony.

5.2.1.2 Reichert's Cartilage

Reichert's cartilage has one extraordinary feature: a long, pointed accessory process which extends from the proximal part of the cartilage (fig. V-1). To my knowledge, this process has not been previously described for another mammal. Unfortunately, the posterior part of the auditory region is not preserved in MPIH 305/E, so its presence in the older fetus cannot be confirmed. I could not identify this accessory process in the adult skulls of E. rozeti, although it is possible that it remains cartilaginous and was lost during maceration. The process is not mentioned by any of the workers who have investigated the development of the macroscelidean auditory region (VAN DER KLAAUW 1929; SPRAGUE 1944; FINDLAY 1944; ROUX 1947).

Both VAN DER KLAAUW (1929) and FINDLAY (1944) have found a cartilage of Spence which conducted the chorda tympani into the tympanic cavity (see 5.4.3) in most of their specimens. Although it cannot be completely discounted that the accessory process is a cartilage of Spence, this seems doubtful since it does not contact the chorda tympani (fig. V-12).

If the process is not simply an anomaly of MPIH 311/E1, then the only explanation I can offer for its presence is that it functions as an additional support for the hyoid musculature.

The distal portion of Reichert's cartilage is extensively ossified by the stylohyal center in both fetuses. The tympanohyal is continuous with the petrosal (crista parotica), protrematic in position and accommodated within a vagina processi hyoidei in the adult (SPRAGUE 1944). ROUX (1947:258) was able to distinguish a separate center for the tympanohyal in E. myurus.

5.2.2 EPITYMPANIC WING OF THE SPHENOID

The epitympanic wing of the sphenoid consists of a large outgrowth from the alisphenoid and a small contribution from the basisphenoid around the foramen caroticum primitivum (or anterior carotid foramen). However, unlike the equivalent formation in Tupaia glis (see figs. IV-3, IV-4), the wing is not covered by the entotympanic in elephant shrews.

The epitympanic wing develops intramembranously, as usual. In MPIH 311/E1, it is still distantly separated from the tegmen tympani and epitympanic wing of the petrosal (fig. V-1), but in MPIH 305/E these processes are in articulation and form the lengthy petrosphenoid suture.

The only prominent features on the undersurface of the wing are the tympanic aperture of the pterygoid canal and the eminence between diverticular Da and Db (which accommodates the trigeminal ganglion as well as the ramus inferior).

5.2.3 EPITYMPANIC WING OF THE SQUAMOSAL

Only the entoglenoid process of the squamosal plays any significant part in the bounding of the middle ear (see 5.1.10). An epitympanic wing does not form at all, and thus the squamosal does not appear in the roof of the tympanic cavity (fig. V-2).

There is nothing unusual about the development of the squamosal. The squamosal does not completely cover the pars canalicularis of the petrosal (contra ROUX 1947:271). The small process in the posterior wall of the external auditory canal which covers the foramen stylomastoideum definitivum (fig. V-2, V-3) is a 'mastoid' process in the sense of VAN KAMPEN (1905) and not a posttympanic process (i.e., it is derived from the petrosal rather than the squamosal). A postglenoid process can be definitely identified in the adult (*contra* ROUX 1947 and MCDOWELL 1958), although it is small. It may not be formed in secondary cartilage (as is commonly the case), since this tissue was not found at the rear of the glenoid fossa in either of the two fetuses of *E. fuscipes*.

5.3 PRINCIPAL SPACES AND SEPTA OF THE MIDDLE EAR

The degree of pneumatization of the middle ear varies widely among the Macroscelidea (VAN KAMPEN 1905; EVANS 1942). Accordingly, the descriptions in this section will apply only to *Elephantulus* except where noted otherwise.

Although some species of *Macroscelides* are said to have large accessory cavities which inflate the whole rear of the skull (VAN KAMPEN 1905; KEEN and GROBBELAAR 1941), these are entirely absent in *Elephantulus*. Even a rudimentary mastoid cavity of the sort found in *Tupaia* is lacking, and therefore it is necessary to describe only the hypotympanic sinus and epitympanic recess.

All septa are low and insignificant.

5.3.1 PRINCIPAL SPACES

5.3.1.1 Hypotympanic Sinus

The hypotympanic sinus is large in all elephant shrews. EVANS (1942) claims that the bullae of *Elephantulus* are the largest in comparison to total skull length, but this is probably incorrect (cf. THOMAS and SCHWANN 1906). EVANS did not study *Macroscelides*, which is usually considered to have the most voluminous bullae (EVANS' '*Macroscelides*' *rozeti* is properly *Elephantulus rozeti*). The great size of the macroscelidean bulla is mostly due to the extensive inflation of its anterior portion (see figs. V-2, V-3).

SABAN (1956-57:82) recognizes three diverticula of the hypotympanic sinus (Da, Db, and D_3). As noted previously (see 2.3.1), D_3 includes the saccus posterior and should be included within the true tympanic cavity. Diverticula Da and Db are not regarded as the equivalents of D_1 and D_2 of strepsirhines and tree shrews by SABAN because they are formed by the alisphenoid and basisphenoid.

The alisphenoid (alisphenoidal part of the epitympanic wing of the sphenoid and tympanic process of the alisphenoid) forms the bony walls of diverticulum Da (fig. V-2) except for a small area completed by the entoglenoid process of the squamosal. Two incomplete septa further delimit this space according to SABAN (1956-57). One is dorsal in position and is erected on the petrosphenoid suture of the roof of the tympanic cavity. The other is ventral, and arises from the margins of the suture between the ectotympanic and tympanic process of the alisphenoid. In *Elephantulus*, however, the dorsal septum is absent and the margins of the petrosphenoid suture are flat.

SABAN also claims that this diverticulum is additionally bounded by a delicate membrane stretching between the dorsal and ventral septa. There is no sign of this membrane in either fetus of E. fuscipes, and it is not present in the macerated skulls of adult E. rozeti. I suspect that this membrane is only a shrunken remnant of the mucous tunica mucosa of the tympanic cavity, a common artefact of incompletely macerated skulls.

Diverticulum Db is restricted to the small loculus medial to the canal for the ramus inferior (fig. V-2). The ontogenetic evidence supports SABAN's (1956-57:82) conclusion that the roof of this diverticulum is formed by the basisphenoid (i.e., basisphenoidal part of the epitympanic wing of the sphenoid).

It is also necessary to note that the hypotympanic sinus extends along most of the medial side of the promontory in the adult, as a result of the pneumatization and medial migration of the petrosal plate.

Diverticulum D_3 is bounded medially by a small posterior septum which conducts the internal carotid to the promontory. Diverticulum D_3 appears to inflate slightly during ontogeny, but it is the smallest of the three identified by SABAN.

As in strepsirhines and tree shrews, the hypotympanic sinus does not inflate significantly until after birth. Diverticulum Da is very small in MPIH 305/E, and Db is not yet represented.

5.3.1.2 Epitympanic Recess

The epitympanic sinus is bounded medially by the proximal stapedial artery, posteriorly by the prominence of the lateral semicircular canal and the facial canal, and laterally and anteriorly by the anterior crus of the ectotympanic (fig. V-2). It is entirely formed by the tegmen tympani, there being no epitympanic wing of the squamosal (see 5.2.3). It is broad but very shallow, and evidently undergoes only a small degree of inflation.

The mastoid cavity and accessory spaces are completely absent in Elephantulus.

5.3.2 PRINCIPAL SEPTA

The septa of the middle ear require little comment. None of them are complete, and all are related to blood vessels or sutures. In addition to those described in the preceding section, there is a small [?anterior] septum which conducts the promontorial artery from the anterior pole of the promontory to the anterior carotid foramen (fig. V-2). A small septum also ranges along the suture between the petrosal plate and the caudal entotympanic.

5.4 MUSCLES, ARTERIES AND NERVES OF THE MIDDLE EAR

5.4.1 OSSICULAR MUSCLES

The tensor tympani originates from a small fossa between the canal for the proximal stapedial and the lateral wall of the promontory (fig. V-1, V-2). It presents no unusual features and is supplied as usual by the otic ganglion. It inserts into the malleus by means of a single tendon.

The stapedius muscle has an extratympanic site of origin throughout ontogeny. It arises from the side-wall of the skull beneath the prominence of the lateral semicircular canal; a foramen in the dorsal part of the CTPP (fig. V-2) conducts it into the distal part of the facial canal. Its tendon leaves the facial canal through a small foramen in order to enter the tympanic cavity and insert on the stapes. The muscle is supplied by the VIIth nerve.

The element of Paaw is absent in MPIH 311/E1 and in the specimens studied by VAN DER KLAAUW (1929).

5.4.2 ARTERIES

5.4.2.1 Introduction

Relatively complete descriptions of the internal carotid system are reported in BUGGE (1972, 1974; for *E. rozeti*) and SABAN (1956-57; for '*Macroscelides*'). Incidental observations can be found in a number of papers, but these are usually very brief and often refer only to foramina of entry and exit (e.g., VAN KAMPEN 1905; CARLSSON 1909; VAN DER KLAAUW 1931; EVANS 1942; BUTLER 1956; MCDOWELL 1958).

On the whole, it appears that *Elephantulus* is the only macroscelidean which can be considered well-known, and the extent of variation (if any) within the order has never been ascertained. Little that is new can be presented in this section, since description is likewise based on species of the same genus.

The stem and major branches of the internal carotid are illustrated in fig. V-1 for fetal _E_. _fuscipes_.

5.4.2.2 Stem and Major Tympanic Branches of the Internal Carotid Artery in E. fuscipes and E. rozeti

The internal carotid enters the tympanic cavity in company with the internal carotid nerve and gains the promontory medial to the apetura fossulae fenestrae cochleae. It almost immediately bifurcates thereafter into the proximal stapedial and promontorial arteries.

The promontorial artery is the smaller of the two, at least in the specimens of _E_. _fuscipes_ where luminal diameters could be checked. This artery passes anteromedially over the promontory in a broad but shallow sulcus,grooves the epitympanic wing of the petrosal in front of the anterior pole, then leaves the tympanic cavity for the circulus arteriosus. There is no vidian branch (artery of the pterygoid canal).

A large vein bound for the cavernous sinus accompanies the promontorial artery through the anterior carotid foramen (figs. V-19, V-20); this probably accounts for the relatively large size of the foramen in the adult (fig. V-2).

The proximal stapedial is very large. It is equal in size to the internal carotid and its luminal diameter is one and one-half (MPIH 305/E) to two (MPIH 311/E1) times that of the promontorial artery. There is no ramus posterior.

The proximal stapedial passes through the stapes, crosses the facial nerve, then fiburcates into its two major branches (ramus superior and inferior) adjacent to the tensor tympani fossa. The two rami are approximately equal in size in the specimens of E. fuscipes and have luminal diameters which are two-thirds that of the parent vessel.

The ramus superior immediately passes laterally and dorsally out of the tympanic cavity to form the middle meningeal artery.

The ramus inferior strikes anteromedially across the anterior part of the tegmen tympani in company with the lesser petrosal nerve and a small vein (fig. V-17). At the site of the petrosphenoid suture it rises to the cerebral surface of the epitympanic wing of the sphenoid and enters a long, capacious groove which accommodates the trigeminal ganglion and nerve V_3. It enters the temporal fossa adjacent to the foramen ovale and continues forwards as the infra-orbital ramus (BUGGE 1974).

Differences from T. glis (4.4.2) include relatively larger size and a somewhat different route, for the ramus inferior in Elephantulus does not pass through the Glaserian fissure. Also, the vessel does not anastomize with the 'internal' maxillary artery.

5.4.2.3 Relative Size of the Promontorial and Stapedial Arteries

BUGGE (1974:25) concludes that there is an incipient reduction of the stapedial artery in favor of the external carotid system, since the anastomosis with the 'internal' maxillary is lost and the mandibular artery is supplied by the external carotid alone.

Nonetheless, the proximal stapedial is not a small vessel, and is only moderately smaller than the external carotid in the sectioned specimens. This situation may alter with further development, however. The rami of the stapedial are obviously not reduced.

However, the vertebral-basilar system is evidently more significant for cerebral irrigation than the internal carotid is. The basilar artery was found to be nearly twice the size of the promontorial artery in the sectioned specimens. This, combined with the fact that the promontorial artery is also smaller than the proximal stapedial, suggests that the former is undergoing reduction in Elephantulus. Adult conditions cannot be determined with accuracy because the promontorial artery is not enclosed in a canal and the anterior carotid foramen provides passage for part of the deep petrosal nerve and a large vein as well as the promontorial artery.

It should be noted that BUGGE (1974:313, table 1) reaches a different conclusion. He feels that the vertebral-basilar system and the internal carotid supply the brain in equal measure.

5.4.2.4 Canals and Foramina

In adult E. rozeti bony canals surround the ramus superior and inferior and most of the proximal stapedial (fig. V-2).

The proximal stapedial is unenclosed until it leaves the obturator foramen of the stapes. It passes directly through the facial canal, then diverges anteriorly within its own tube. After a short course along the roof of the tympanic cavity the stapedial canal bifurcates into the canals for the ramus superior and inferior.

The petrosal forms the canals for the stapedial and ramus superior, and most of the canal for the ramus inferior. SABAN (1956-57: 78, fig. 36B) illustrates a long canal for the ramus inferior on the epitympanic wing of the sphenoid. Actually, the elevation which appears on the ventral surface of this wing is mostly produced by the trigeminal fossa and nerve V_3. The ramus superior enters the trigeminal fossa in front of the petrosphenoid suture in both fetus and adult (fig. V-15).

The dorsal surfaces of the canals for the ramus inferior and superior are fenestrated, but they are always complete ventrally.

The internal carotid and promontorial arteries are contained in sulci, not canals. The posterior septum guides the internal carotid to the promontory, while the anterior septum similarly guides the promontorial artery to the anterior carotid foramen.

In E. fuscipes the posterior carotid foramen lies entirely within the petrosal plate. This is the common position for Macroscelidinae according to EVANS (1942), although CARLSSON (1909) mentions that the foramen perforates the suture between the petrosal plate and the caudal entotympanic in Macroscelides typicus. This is also the case in Rhynchocyon cirnei (VAN KAMPEN 1905).

In the fetus the internal carotid enters the tympanic cavity posteromedially (vig. V-1), while in the adult it enters directly from the posterior (fig. V-2). This ontogenetic shift in position is a consequence of the medial inflation of the posterior part of the petrosal plate. A similar phenomenon occurs in lemurs (see 2.4.2).

An alicochlear commissure is found in prenatal *E. fuscipes* (fig. V-1), and a complete foramen caroticum primitivum is thus produced.

In MPIH 311/E1 the alicochlear commissure is already degenerating, and in MPIH 305/E it has been entirely resorbed. In the adult, the anterior carotid foramen lies in the medial part of the petrosphenoid suture (fig. V-2).

5.4.3 NERVES

The major nerves traversing the tympanic cavity are illustrated in fig. V-1 for fetal *E. fuscipes*. Because of the degree of damage to MPIH 305/E, nerve routes could only be partially studied. Foramina of entry and exit (as they appear in the adult *E. rozeti*) are illustrated in fig. V-2.

(1) Facial (VII) Nerve

In the younger fetus (MPIH 311/E1) the facial nerve follows a typical route from the cavum supracochleare across the roof of the tympanic cavity to the foramen stylomastoideum primitivum. It is contained within a deep sulcus which it shares anteriorly with the stapedial artery and posteriorly with the stapedius muscle.

In the adult, the nerve is enclosed in a complete canal. The stapedius muscle perforates the distal part of the canal in order to enter the tympanic cavity, while the stapedial artery enters the proximal part through a foramen adjacent to the fenestra vestibuli. There is a complete foramen stylomastoideum in the adult.

(2) Chorda Tympani

The chorda tympani is given off by the VII nerve as it leaves the auditory capsule. In the fetus, it travels underneath Reichert's cartilage and enters the tympanic cavity through a membranous foramen. It then passes around the malleus, notches the gonial, and leaves the tympani cavity over the anterior crus of the ectotympanic.

In the adult, the chorda tympani passes between the ectotympanic and entoglenoid process of the squamosal (Glaserian fissure). No separate canaliculus chordae tympani was identifiable.

VAN DER KLAAUW (1929) found an element of Spence in six of his seven specimens. The presence of this element in Elephantulus myurus has been independently confirmed by FINDLAY (1944). The element of Spence conducts the chorda tympani over the posterior crus of the ectotympanic into the tympanic cavity. This cartilage is absent in MPIH 311/E1, unless it be represented by the accessory process on Reichert's cartilage (see 5.2.1). The relevant region in MPIH 305/E is not preserved.

(3) Internal Carotid Nerve and Deep Petrosal

The internal carotid nerve is large and arises as usual from the cranial cervical ganglion. It divides into two major branches and follows the internal carotid into the tympanic cavity. Both branches remain in close relation to the promontorial artery. One branch follows the latter through the anterior carotid foramen; the other (as the deep petrosal) follows the greater petrosal to the pterygoid canal.

(4) Greater Petrosal

The nerve arises from the geniculate ganglion and passes along a groove on the cerebral surface of the epitympanic wing of the petrosal. In the younger fetus, it passes over this wing into the piriform fenestra, where it meets the deep petrosal.

In the older fetus and in the adult, the greater petrosal passes into the tympanic cavity through a foramen located in the petrosphenoid suture.

(5) Nerves of the Pterygoid Canal

The deep and greater petrosal nerves cross the roof of diverticulum Db to the tympanic aperture of the pterygoid canal.

(6) Auricular Ramus of the Vagus

In MPIH 311/E1, the auricular ramus does not perforate the fibrous membrane of the tympanic cavity, but instead passes around it and enters the (extratympanic) stapedius fossa. It attains the facial nerve at the foramen stylomastoideum primitivum.

Judging from fetal conditions, the route of the auricular ramus should be extratympanic in the adult Elephantulus. However, SABAN (1956-57:60) states that there is a mastoid canaliculus in the petrosal in adult Rhynchocyon.

(7) Tympanic Nerve and Lesser Petrosal

In the younger fetus, the tympanic nerve passes laterally over the CTPP in company with the auricular ramus of the vagus. Unlike the latter, it perforates the fibrous membrane of the tympanic cavity, then follows a typical route through D_3, over the proximal stapedial artery, and along the promontory.

The nerve enters a small tympanic plexus in the anterior part of the tympanic cavity and travels anteriorly (as the lesser petrosal) in close association with the ramus inferior of the stapedial. In MPIH 305/E and the adult the lesser petrosal enters the canal of the ramus inferior by passing through the petrosphenoid suture. It then enters the trigeminal fossa and attains the otic ganglion.

The CTPP was not preserved in MPIH 305/E, and the position of the foramen of entry for the tympanic nerve (the tympanic canaliculus) could not be determined. In the adult, there appears to be a small foramen at the base of the CTPP just medial to the aperture which permits the stapedius muscle to enter the tympanic cavity from the stapedius fossa. This may accommodate the tympanic nerve, although its position is more anterior than one would expect from fetal conditions. Failing this, the nerve may enter the tympanic cavity through the suture between the petrosal plate and the caudal entotympanic (cf. conditions in _T_. _glis_, section 4.4.3).

ROUX (1947:252, 253; figs. 29, 30) mistakenly identifies one of the two branches of the internal carotid nerve as the "lesser superficial petrosal".

5.5 SUMMARY OF PRINCIPAL FINDINGS

(1) The rostral and caudal entotympanics both arise within the fibrous membrane of the tympanic cavity, which forms the original

ventral wall of the middle ear.

(2) Numerous bones lie in or contribute to the bullar wall of the adult macroscelidean: the alisphenoid, basisphenoid, posterior part of the pterygoid, caudal and rostral tympanic processes of the petrosal, entoglenoid region of the squamosal, ectotympanic, and the rostral and caudal entotympanics. The rostral entotympanic may remain cartilaginous into adult life. According to the interpretation advanced here, the caudal entotympanic arises as a peculiar form of membrane bone.

(3) The ectotympanic is considerably broadened to the lateral in the adult, and is fused to the caudal entotympanic.

(4) The ectotympanic is phaneric and maintains an edge-to-edge articulation with the tympanic process of the alisphenoid and caudal entotympanic throughout ontogeny, although it only fuses with the latter.

(5) The epitympanic wing of the sphenoid forms the anterior part of the roof of the middle ear, while the epitympanic wing of the petrosal and the tegmen tympani form the posterior part. The epitympanic wing of the squamosal is entirely lacking. The anterior crus of the ectotympanic, which is very long, forms the superior wall of the external acoustic meatus. The entotympanics do not contribute to the roofing of the middle ear.

(6) The piriform fenestra is closed over the in the adult except for the small gap represented by the petrosphenoid suture.

(7) The hypotympanic sinus is large, but other cavities are negligible in size. Septa are rudimentary.

(8) The origin of the stapedius muscle lies outside the tympanic cavity throughout ontogeny. There is nothing unusual about the routes of the arteries and nerves selected for study.

CHAPTER SIX

ERINACEOMORPHA

METHOD OF DESCRIPTION

6.1 VENTRAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

- 6.1.1 Fibrous Membrane of the Tympanic Cavity
- 6.1.2 Cartilage of the Auditory Tube
- 6.1.3 Tympanic Processes of the Petrosal
- 6.1.4 Ectotympanic
- 6.1.5 Tympanic Process of the Basisphenoid
- 6.1.6 Relationship of the Ectotympanic and Tympanic Process of the Basisphenoid
- 6.1.7 Other Tympanic Processes

6.2 DORSAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

- 6.2.1 Tegmen Tympani, Epitympanic Wing of the Petrosal, and Reichert's Cartilage
- 6.2.2 Epitympanic Wing of the Sphenoid
- 6.2.3 Epitympanic Wing of the Squamosal

6.3 PRINCIPAL SPACES AND SEPTA OF THE MIDDLE EAR

- 6.3.1 Principal Spaces
- 6.3.2 Principal Septa

6.4 MUSCLES, ARTERIES AND NERVES OF THE MIDDLE EAR

- 6.4.1 Ossicular Muscles
- 6.4.2 Arteries
- 6.4.3 Nerves

6.5 SUMMARY OF PRINCIPAL FINDINGS

6.1 VENTRAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

Unlike the mammals discussed in previous chapters, the ventral wall is not covered by a smooth, continuous shell of bone in modern Erinaceidae. Membrane completes the anterior and posterior sides of the middle ear cavity.

The largest tympanic process in the ventral wall arises from the basisphenoid. Smaller contributions come from the petrosal, alisphenoid, pterygoid and squamosal (in addition to the ectotympanic). The entotympanics are not represented.

In Talpidae and at least some fossil erinaceids, bullar development tends to be more complete.

6.1.1 FIBROUS MEMBRANE OF THE TYMPANIC CAVITY

The fibrous membrane is present in all specimens, but is indistinctly stained in all but the young infant (MPIH 1966/146).

Its relations differ from those described in previous chapters in only one significant respect. Instead of closely investing the anteromedial surface of the promontory, the fibrous membrane simply curves around it (fig. VI-6), after leaving the central stem. However, this more medial placement is readily explainable when reference is made to the relationship of the fibrous membrane and periosteal outgrowths in other mammals (e.g., tympanic processes of the petrosal in strepsirhines; see 2.1.3, 3.1.3). Such outgrowths consistently grow along the intratympanic surface of the fibrous membrane; but

Table 6-1

ERINACEOMORPHA

SPECIMENS	No.	CRL[1]	HL[2]	ST[3]	PS[4]	STAINS
ERINACEINAE						
Erinaceus europaeus						
I. Near-Term Fetus	MPIH 1964/58a	28.0	13.0	10	cross	Klüver-Barrera
II. Newborn	MPIH 1964/52b	48.0	20.0	10	cross	Klüver-Barrera
III. 4 Days Postnatal	MPIH 1964/57	50.0	--	10	cross	Klüver-Barrera
IV. Young Infant	MPIH 1966/146	--	--	10	cross	Azan

[1] Crown-rump length (in mm)

[2] Head length (in mm)

[3] Section thickness (in mμ)

[4] Plane of sectioning

NOTES ON SPECIMENS

The young specimens of Erinaceus europaeus were collected from females captured in the environs of Frankfurt/M.

Three of the specimens had been stained by the Klüver-Barrera method, a nerve-fiber staining procedure which visualizes connective tissues poorly. Accordingly, structural descriptions rely heavily on the oldest, Azan-stained specimen (MPIH 1966/146).

Adult skulls of E. europaeus from the personal collection of Dr. W.B. SPATZ (Neurobiologische Abteilung, MPIH) were also available for study.

if the disposition of the membrane in *Erinaceus* were similar to that displayed by *Microcebus*, for example, the tympanic process of the basisphenoid would like outside the presumptive tympanic cavity. It does not, however, because of the different placement of the fibrous membrane.

As in the other non-strepsirhine forms discussed here, the origin of the stapedius muscle lies outside the presumptive tympanic cavity as defined by the attachments of the fibrous membrane and the positioning of the CTPP (fig. VI-18a,b,c). Consequently, the muscle must bore through the membrane in order to gain the stapes.

6.1.2 CARTILAGE OF THE AUDITORY TUBE

The cartilage of the tube is completely absent in the near-term fetus (MPIH 1964/58a) and only developed to a rudimentary extent in the three post-natal specimens. It consists of a short, flat bar of cartilage on the dorsal side of the auditory tube which lies immediately below the posterior extremity of the pterygoid bone. In the adult, there is a slight depression where the tympanic processes of the basisphenoid and the alisphenoid adjoin (fig. VI-1). This depression accommodates the cartilage of the tube during life.

No accessory cartilages were found in the sectioned specimens, and both entotympanics are evidently absent in hedgehogs. SPRAGUE (1944:178) makes the extraordinary statement that in *Echinosorex* there is an entotympanic bulla which completely envelops the ectotympanic. This is inaccurate; only the tympanic wing of the basisphenoid is present in that genus (see fig. 3 in BUTLER 1948:449).

6.1.3 TYMPANIC PROCESSES OF THE PETROSAL

6.1.3.1 Introduction

The recent studies by GAWNE (1968) and RICH and RICH (1971) have established that Erinaceidae are more variable in otic anatomy than previously thought. Variability in the tympanic processes of the petrosal is quite evident, especially when fossil forms are considered. In Brachyerix (Miocene, N.A.), for example, the petrosal (together with the sphenoid and ectotympanic) helps to form a definite auditory bulla which is far more complete than in any contemporary hedgehog. The disposition of the petrosal contribution in this genus suggests that both rostral and caudal processes were formed, a situation which is also found in Erinaceus europaeus and, presumably, in other modern erinaceids. However, in living forms these processes are not enlarged to the degree seen in Brachyerix.

A tympanic process of the petrosal has been described for Erinaceus and its allies by a number of authors, although their descriptions do not entirely conform to one another. For LECHE (1902), the process consisted of a narrow ridge adjoining the posterior margin of the basisphenoid. In addition to LECHE's process, VAN KAMPEN (1905) described another small outgrowth directly posterior to the sulcus for the internal carotid artery. He regarded both outgrowths as a structural unit, subdivided by a deep incisure for the internal carotid. BUTLER (1956), in the course of a general description of the erinaceid auditory region, described what appears to be yet another petrosal process. This one was said to cover the apertura fossulae fenestrae cochleae from the rear and to make contact with the tympanohyal.

Examination of both young and adult stages of E. europaeus establishes that all three of these projections are typically present in that species (fig. VI-1). The anterior one, which articulates with the tympanic process of the basisphenoid, is a rostral tympanic process of the petrosal. The other two may be regarded together as the caudal tympanic process of the petrosal.

6.1.3.2 Caudal Tympanic Process of the Petrosal

The CTPP has complicated relations; its disposition in the fetus and later young stages (see table 6-1) are easier to comprehend if adult conditions are described first. In fig. VI-1 it can be seen that the margins of the apertura fossulae fenestrae cochleae are ringed by a series of lips and flanges. There are two major outgrowths, and these conform to the medial and lateral sections of the CTPP as previously defined (see 1.4.3 and fig. I-2). The medial section lies directly behind the sulcus for the internal carotid and arises from the medial wall of the apertura. It is separated from the lateral section of the CTPP by a broad gap which communicates with the posterior lacerate foramen. The lateral section is pyramidal in shape and extends from the lateral wall of the apertura fossulae fenestrae cochleae and the area immediately behind the apertura fenestrae vestibuli. In some cases it makes contact with the tympanohyal, but this is a variable feature.

Both sections of the CTPP arise as cartilaginous outgrowths of the auditory capsule. The lateral section is often the larger and is better developed of the two in young stages. In MPIH 1964/57 (4 days old), it begins directly behind the apertura fenestrae vestibuli and extends posteriorly along the ventral surface of pars canalicularis, always on the internal side of the stapedius muscle and facial nerve (figs. VI-8, VI-9, VI-10). In the young infant (MPIH 1966/146) it has the same relations and is slightly larger (figs. VI-15, VI-16, VI-17, VI-18). It should be noted that the hypothetical mammal illustrated in fig. I-2 is shown as having a very broad canalicular portion of the petrosal. In *E. europaeus* this area is relatively constricted; the lateral section of the CTPP (in this case, conforming to 5c' in fig. I-2) is situated more medially and thus touches the rear of the apertura fenestrae vestibuli.

The medial section arises as a ventrolateral extension of the processus recessus (which later becomes the medial wall of the apertura fossulae fenestrae cochleae). It cannot be usefully distinguished from the processus recessus until after birth (cf. fig. VI-10c and figs. 18a,b). As in the adult, there is a marked gap between the medial and lateral sections. Neither section is ossified even in the young infant.

The CTPP is present in all modern erinaceids according to BUTLER (1956); whether it is always bilobate is not clear from his descriptions. It is apparently not in *Paraechinus aethiopicus*, judging from the illustration in RICH and RICH (1971:53, fig. 22). The CTPP does not meet the posterior crus of the ectotympanic, at least in *E. europaeus*.

6.1.3.3 Rostral Tympanic Process of the Petrosal

A RTPP of small size is evidently common in Erinaceidae (see BUTLER 1956), but there is no sign of it in the available young specimens of E. europaeus. This is no doubt due to its method of origin, for it probably arises as a periosteal outgrowth of the ventral surface of the promontory (as in, for example, Macroscelidea, Lemuriformes, Lorisiformes). However, this part of the auditory capsule is still unossified in the young infant (MPIH 1966/146), and, accordingly, the RTPP is unrepresented.

In the adult E. europaeus, the RTPP is a stout, short process which completes a small portion of the medioventral wall of the tympanic cavity (fig. VI-1). The suture between the tympanic process of the basisphenoid and the RTPP can usually be distinguished in well-cleaned skulls. The ventral margin of the RTPP displays a small facet for the ectotympanic. Note that only a restricted part of the zone which gives rise to the RTPP in strepsirhines is competent to produce an outgrowth in Erinaceus (see also fig. I-2).

In modern hedgehogs, the tympanic processes of the petrosal are little affected by pneumatization and do not markedly increase in size during postnatal life. The extinct form Brachyerix is strikingly different in this respect. A large petrosal plate (presumably consisting of the coalesced RTPP and CTPP) shields the entire posterior part of the tympanic cavity. Further, it is quite likely that the plate is not in its original ontogenetic position (i.e., it has migrated medially as a result of pneumatic activity; cf.

conditions in Lemuriformes, 2.1.3), for the medial surface of the promontory is exposed within the tympanic cavity (see RICH and RICH 1971:36, fig. 17).

6.1.4 ECTOTYMPANIC

6.1.4.1 Structure, Relations and Development

The ectotympanic is broadened medially in the Erinaceinae, although it remains slender in some members of the Echinosoricinae (BUTLER 1948). BUTLER (1948:454) records that an anterior process of the ectotympanic is present in some erinaceids (e.g., Hylomys, Neotetrachus; cf. Ptilocercus lowii, fig. IV-42), but SABAN (1956-57:62) states that this process is simply the gonial projecting beyond the anterior crus of the ectotympanic.

In young stages of E. europaeus the ectotympanic has the shape of a flattened, incomplete ring. The apical region of the anterior crus is broadened and receives the gonial and Meckel's cartilage in a capacious sulcus malleolaris (figs. VI-3, VI-4). In the young infant (MPIH 1966/146) the ectotympanic is highly trabeculated and consists of young woven bone rather than 'intermediate' bone (cf. 2.1.5). Its lateral rim is not particularly broadened even at this stage of development. The ectotympanic lies free of all other skeletal elements.

In the adult, medial broadening of the ectotympanic is pronounced (fig. VI-2). The bone is tightly bound to the tympanic process of the basisphenoid by fibrous tissue (derived from the fibrous membrane of the tympanic cavity). Fibrous tissue also binds it to the RTPP. The ectotympanic does not entirely fill the ventrolateral wall of the tympanic cavity, which is completed dorsally by the flaccid portion of the tympanic membrane (BONDY 1907; HENSON 1961).

The gonial is not fused to the malleolar sulcus in hedgehogs according to HENSON (1961) and WASSIF (1948).

6.1.4.2 Inclination of the Ectotympanic

The ectotympanic rotates little during ontogeny in *E. europaeus* (see table 6-2). This is not surprising, considering the tenuous links the ectotympanic has with both the dorsal wall and the tympanic process of the basisphenoid. Nonetheless, some degree of displacement must occur since the ectotympanic is separated by a wide interval from the ventral surface of the promontory in the mature animal.

Inclination values of 20° and 23° have been reported for adult *Erinaceus* by SABAN (1956-57) and HENSON (1961) respectively.

6.1.5 TYMPANIC PROCESS OF THE BASISPHENOID

The tympanic process of the basisphenoid is found in all recent Erinaceidae (VAN KAMPEN 1905; VAN DER KLAAUW 1931; BUTLER 1948).

In the adult *E. europaeus*, the tympanic process flares downwards and backwards from the basisphenoid to cover a portion of the promontory and the rim of the ectotympanic (fig. VI-2). The height of the process is exaggerated anteriorly in Erinaceinae by the deep basisphenoid pit, a feature which is absent in Echinosoricinae (BUTLER 1948:456). The tympanic process of the basisphenoid terminates anatomically at the site of the gutter for the cartilage of the tube

Table 6-2

INCLINATION OF THE ECTOTYMPANIC IN YOUNG ERINACEOMORPHA

Specimen No.	Angle of Inclination L	Angle of Inclination R	Average Inclination
Erinaceus europaeus			
MPIH 1964/58a	10°	12°	11.0°
MPIH 1964/52b	18°	22°	20.0°
MPIH 1964/57	17°	18°	17.5°
MPIH 1966/146	14°	15°	14.5°

For computation of the angle of inclination, see note accompanying table 2-2.

(see below). Posteriorly, the process abuts the RTPP, with which it can be partly fused.

The basisphenoid center is small in the three younger sectioned specimens, and the tympanic process consists of a ridge of trabeculae projecting ventrally. The process is slightly more developed in MPIH 1966/146 (young infant), but it does not yet project over the promontory (fig. 13a,b). It clearly arises as a periosteal outgrowth of the basisphenoid and never has a separate existence.

The pterygoid bone completes the area where the tympanic process of the basisphenoid becomes confluent with the tympanic wing of the alisphenoid (i.e., the region traversed by the gutter for the auditory tube), judging from conditions in young stages (figs. VI-3, VI-11).

6.1.6 RELATIONSHIP OF THE ECTOTYMPANIC AND TYMPANIC PROCESS OF THE BASISPHENOID

In adult hedgehogs the ectotympanic is in broad contact with the leading edge of the tympanic process of the basisphenoid. In _E_. _europaeus_, this process actually overlaps the ectotympanic to a small extent (semiphaneric condition; fig. VI-2). Synostotic union of the two does not occur.

In the oldest available sectioned specimen (MPIH 1966/146), the tympanic process of the basisphenoid and the ectotympanic are not yet in close proximity (fig. VI-13b). All that unites them is the fibrous membrane of the tympanic cavity; whether there are sutural tissues between the bone territories in the adult is unknown.

SABAN (1956-57:86-87) claims that there is an 'external anulus membrane' in erinaceids which joins the tympanic process of the basisphenoid to the ectotympanic. This membrane is described as being "cartilaginous". By its position and relations, the 'anulus membrane' which SABAN illustrates (1956-57:87, fig. 39A) can only be the fibrous membrane of the tympanic cavity (with perhaps some of the membranous meatus included as well).

The tympanic process of the basisphenoid is clearly in a position to surround the ectotympanic in _E_. _europaeus_, but no cases of a completely aphaneric ectotympanic enclosed within a tympanic process of the basisphenoid are known in the erinaceomorph fossil record. However, it would appear that there has been at least one instance of the fusion of the ectotympanic with surrounding tympanic processes in the evolution of hedgehogs. This is the Miocene form _Brachyerix_, in which the ectotympanic cannot be separated from the other bullar components (see RICH and RICH 1971).

6.1.7 OTHER TYMPANIC PROCESSES

6.1.7.1 _Tympanic Process of the Alisphenoid_

A discontinuous rampart of bone defines the anterior limit of the middle ear cavity in adult erinaceids. This ridge is the 'preotic crest' of MCDOWELL (1958) and consists of both sphenoidal and squamosal elements.

Conditions in the sectioned specimens suggest that the pterygoid bone contributes to the part of the ridge accommodating the gutter for the cartilage of the tube (and adjoining the tympanic process of the basisphenoid; see fig. VI-1). The lateral part of the ridge, which surrounds the incisure for the ramus inferior, is entirely alisphenoidal in origin. The basis for this conclusion is illustrated in fig. VI-11. Although the pterygoid is completely fused to the basisphenoid in MPIH 1966/146 (young infant), the division between them lies along the track of the nerves of the pterygoid canal. The bone ventral to the canal is pterygoidal in origin, and it forms the thick, projecting shelf which covers the pterygoid canal in the adult (fig. VI-1).

According to BUTLER (1948:456), the tympanic process of the alisphenoid reaches laterally as far as the postglenoid foramen in Echinosoricinae, but not in Erinaceidae. In some cases, the incisure for the ramus inferior becomes a complete foramen (e.g., *Paraechinus aethiopicus*; RICH and RICH 1971).

6.1.7.2 Squamosal

There is a small lamella in *E. europaeus* adults which lies directly behind the postglenoid foramen, in line with the tympanic process of the alisphenoid. Because of the marked lateral broadening of the epitympanic recess (see 6.3.1) and consequent modifications of the squamosal, it is difficult to know whether this lamella should be regarded as an outgrowth of the entoglenoid part of the bone. Since it lies behind the postglenoid foramen, it probably should not. According to HENSON (1961:164), the flaccid portion of the tympanic membrane attaches to this lamella, indicating that it is best regarded as a part of the dorsal margin of the external acoustic meatus.

6.2 DORSAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

The construction of the roof of the tympanic cavity in adult E. europaeus is illustrated in fig. VI-1. The roof is completed anteriorly by the epitympanic wing of the sphenoid and posteriorly by the petrosal. A very small contribution is also made by the epitympanic wing of the squamosal.

There is no suture on the epitympanic wing of the sphenoid, although it undoubtedly consists of both alisphenoidal and basisphenoidal material. The piriform fenestra is closed over except for the narrow gap represented by the petrosphenoid suture.

The investigations of BUTLER (1948) and RICH and RICH (1971) establish that there is little variability in the composition of the dorsal wall in extant or known estinct erinaceomorphs.

6.2.1 TEGMEN TYMPANI, EPITYMPANIC WING OF THE PETROSAL, AND REICHERT'S CARTILAGE

The petrosal contribution to the roof of the tympanic cavity is relatively large in the adult (fig. VI-1), although this is in part due to several modifications of the auditory capsule and its outgrowths. First, the capsules are rotated inwards compared to such forms as lemurs and lorises, which entails a consequent shifting of the pars canalicularis to a more anterior position. If the position of the foramen faciale is regarded as being close to the morphological root of the tegmen tympani, it can be seen that this outgrowth is in fact rather short. Secondly, the epitympanic recess inflates into the mastoid eminence which considerably increases the breadth of the roof of the tympanic cavity.

In the sectioned specimens the tegmen tympani is a small, thick projection which ranges anteriorly between the promontory and the squamosal (figs. VI-5, VI-6, VI-12). Its anterior end is perforated by a large foramen for the ramus superior. The piriform fenestra is large even at four days after birth, and consequently the leading edge of the tegmen tympani and the epitympanic wing of the sphenoid are separated by a wide gap. A posterior continuation of the piriform fenestra separates the medial edge of the tegmen tympani from the lateral wall of the promontory. The tegmen tympani is entirely cartilaginous in all specimens.

A peculiar feature of the three younger specimens is the labyrinthine appearance of the tegmental cartilage (fig. VI-5, VI-6). The cartilage is normal in appearance in the young infant (fig. VI-12), however.

The crista parotica is enormous (figs. VI-14, VI-15); it can be reasonably assumed from its position that it forms (when ossified) the large mastoid eminence characteristic of adult erinaceids (fig. VI-1). The crista parotica has a prominent posterior continuation which defines the lateral wall of the stapedius fossa (figs. VI-18a,b,c).

In the adult, a transverse crest separates the true epitympanic recess (which houses the head of the malleus) from the accessory space which lies in the mastoid eminence (see 6.3.1). This crest is regarded by BUTLER (1956) as the Chordaforsatz of BONDY (1907).

An epitympanic wing of the petrosal was not evident in any of the sectioned specimens, although one may form after the ossification of the promontory. In any event, the interval between the promontory and the tegmen tympani is closed over in the adult.

Reichert's cartilage shows normal relations. In the sectioned specimens it consists of an ample bar of cartilage fused to the crista parotica; it is completely unossified even in the young infant (fig. VI-17).

The tympanohyal and stylohyal are separated by the tympanostyloid cartilage in the adult, which is an unossified part of Reichert's cartilage (SPRAGUE 1944). The tympanohyal is completely exposed in the adult and is in close relation with the posterior crus of ectotympanic and the lateral section of the CTPP (fig. VI-1).

6.2.2 EPITYMPANIC WING OF THE SPHENOID

The epitympanic wing of the sphenoid is large (fig. VI-1) in the adult. The basisphenoid probably forms the section of the wing which lies medial to the anterior carotid foramen, judging from conditions in young specimens (fig. VI-12). Since the tympanic aperture of the pterygoid canal lies at the base of the medial part of the tympanic process of the alisphenoid, the contribution of the pterygoid bone is probably minimal.

The sulcus for the ramus inferior is a prominent feature of the epitympanic wing; the trigeminal fossa does not produce an eminence which is visible from the ventral aspect (cf. Macroscelidea, 5.2.2).

6.2.3 EPITYMPANIC WING OF THE SQUAMOSAL

The squamosal sends out a small epitympanic wing which forms the anterolateral portion of the epitympanic recess (figs. VI-1, VI-6). The postglenoid foramen lies between the tegmen tympani and the squamosal, rather than entirely within the latter bone.

A true postglenoid process is absent according to MCDOWELL (1958), and the large projection adjacent to the mastoid eminence is to be regarded as a posttympanic process. No area of secondary cartilage marks the site of origin of the posttympanic process in the available sectioned specimens.

The small flange which helps bound the anterior limit of the tympanic cavity is discussed in section 6.1.7.

6.3 PRINCIPAL SPACES AND SEPTA OF THE MIDDLE EAR

Pneumatization (as distinct from growth at sutures) exerts only a small influence on the architecture of the erinaceid auditory region. There are no deep recesses excavated into the petrosal (as in strepsirhines), and tympanic processes show little evidence of intense pneumatic activity.

6.3.1 PRINCIPAL SPACES

SABAN (1956-57) does not organize the middle ear cavity into a series of separate diverticula of the sort described for lemurs, lorises, tree shrews and elephant shrews. He recognizes a diverticulum D_3 which lies, as usual, behind the apertura fossulae fenestrae cochleae. He also illustrates for adult Neotetrachus a diverticulum Db in the anteromedial extremity of the middle ear cavity. This diverticulum is supposedly closed off by a membrane, but I suspect he has only seen a detached portion of the mucosal lining of the middle ear (see 5.3.1). However, he is probably correct in assuming that a portion of this part of the cavity is formed by the basisphenoid.

The epitympanic recess is situated in the normal place, but is considerably broadened to the lateral in the adult. I would define the true epitympanic recess as the shallow fossa lying between the small descending process on the squamosal (see 6.1.7), and the ridge which BUTLER (1956) regards as BONDY's *Chordaforsatz*, for this is the space which contains the head of the malleus. A fossa incudis cannot be identified in the adult.

The invagination posterior to the *Chordaforsatz* does not accommodate the auditory ossicles, and I believe that VAN KAMPEN (1905) is correct in regarding this excavation as an accessory space. It lies wholly within the mastoid eminence, but it is difficult to regard it as the equivalent of the mastoid cavity or aditus ad antrum found in strepsirhines and tree shrews.

6.3.2 PRINCIPAL SEPTA

There are no septa of any significance in modern erinaceids. However, it may be noted that the internal carotid, the divisions of the stapedial, and the facial nerve are accommodated within deep sulci in *Erinaceus*. Interestingly enough, the Miocene hedgehog *Brachyerix* possesses a number of well-marked incomplete septa in addition to complete canals around blood vessels (RICH and RICH 1971), indicating that conditions in modern Erinaceus are not necessarily primitive.

6.4 MUSCLES, ARTERIES AND NERVES OF THE MIDDLE EAR

6.4.1 OSSICULAR MUSCLES

Both the tensor tympani and the stapedius are present.

The tensor tympani is large and originates partly from the epitympanic wing of the sphenoid and partly from the petrosal in the area between the anterior pole of the promontory and the sulcus for the ramus inferior. It inserts into the malleus by means of a single tendon and is supplied by a branch from the otic ganglion.

It has already been noted that the origin of the stapedius is extratympanic by virtue of its position medial to the lateral section of the CTPP and fibrous membrane of the tympanic cavity. HENSON (1961:171) finds similar relations in the adult: "the belly of the muscle is embedded in the connective tissue that fills the foramen [stylomastoideum primitivum]; only its tendon is covered with the mucous membrane of the tympanic cavity". The muscle is supplied by the VII nerve, as usual.

The element of Paaw is absent in adult E. europaeus according to HENSON (1961:171); it was not present in any of the sectioned specimens used for this study.

6.4.2 ARTERIES

6.4.2.1 Introduction

The classic description of the cephalic arterial circulation of E. europaeus is that of TANDLER (1899). The general view of most authorities is that Erinaceus and its allies possess an extremely primitive pattern which features (in the case of the tympanic branchings of the internal carotid) large superior and inferior rami of the stapedial and an unreduced promontorial artery (GREGORY 1920; SABAN 1956-57; BUGGE 1974). A vidian branch of the promontorial artery also occurs (BUTLER 1948; RICH and RICH 1971).

Considering the number of accounts of the branchings of the internal carotid in the middle ear made in the last three-quarters of a century, it is remarkable that one branch—the ramus posterior of the stapedial artery--has not been previously described for a modern erinaceid. This branch is present in three of the four sectioned specimens, although there is some evidence that it may obliterate in early postnatal life.

Erinaceinae and Echinosoricinae differ slightly in their cephalic arterial patterns (BUGGE 1974), but they are identical for the vessels of concern here (with the possible exception of the ramus posterior).

Vessels are illustrated in fig. VI-1.

6.4.2.2 Stem and Major Tympanic Branches in the Internal Carotid Artery in *E. europaeus*

The internal carotid is large and enters the tympanic cavity immediately in front of the medial margin of the apertura fossulae fenestrae cochleae. After a short course along the posterior pole of the promontory, it bifurcates into the promontorial and proximal stapedial branches. The proximal stapedial is slightly larger than the promontorial branch in all sectioned specimens and is slightly smaller than the parent vessel.

The promontorial artery crosses the ventral surface of the promontory in a deep sulcus; it then passes over the anterior pole and enters the anterior carotid foramen (foramen caroticum primitivum in young specimens). Just before entering the latter foramen it releases a tiny vidian artery which travels onwards to the pterygoid canal. This branch, which was consistently present in the sectioned specimens, was never more than one-eight the size of the promontorial artery.

The proximal stapedial artery gives off a small ramus posterior in the three younger specimens just before it enters the obturator foramen of the stapes. The ramus is quite small in all cases and has a different distribution from the ramus posterior found in tenrecs and *Solenodon* (see 7.4.2). From its origin it travels beneath the stapes and into the stapedius fossa (figs. VI-7, VI-8, VI-9, VI-10). It spends itself in supplying the stapedius and its investing tissues, for it sends off small rami along its course and cannot be traced posterior to the stapedius fossa. The ramus posterior is replaced by a network of fine arterioles in the young infant (MPIH 1966/146). This may indicate that the vessel undergoes involution during ontogeny and is not normally represented in the adult.

The proximal stapedial continues through the stapes, crosses the VII nerve, then divides into the ramus superior and inferior lateral to the fossa for the tensor tympani. The rami are equal in size and only slightly smaller than the parent vessel. The ramus superior almost immediately passes into the cranial cavity through a foramen situated near the anterolateral edge of the tegmen tympani. The ramus inferior diverges anteriorly beneath the tegmen tympani and the epitympanic wing of the sphenoid. It does not pass through the epitympanic wing in order to gain the trigeminal fossa as in Elephantulus (see 5.4.2) but instead passes out of the tympanic cavity through a notch in the tympanic process of the alisphenoid (cf. similar conditions in soricomorphs, section 7.4.2).

6.4.2.3 Relative Size of the Proximal Stapedial and Promontorial Arteries

The proximal stapedial is slightly larger than the promontorial artery in all sectioned specimens. However, the promontorial artery is as large as each of the two principal rami of the stapedial and cannot be regarded as reduced. The basilar artery is moderately larger than the promontorial artery.

Together, these observations demonstrate that the internal carotid/promontorial and vertebral/basilar systems contribute about equally to the arterial supply of the brain. This is corroborated by TANDLER's (1899, 1902) and BUGGE's (1974) observations on adult E. europaeus.

6.4.2.4 Sulci and Foramina

The tympanic branchings of the internal carotid in Erinaceus lie within deep sulci, not canals.

It may be noted that the proximal stapedial shares a common sulcus with the facial nerve. Also, it is important to mention that a misleading impression of the size of the ramus inferior is given by its sulcus. In the adult, it appears that this ramus must be much larger than the promontorial artery (fig. VI-1), but this is not the case. As may be seen in fig. VI-11, the ramus does not fill the entire volume of the sulcus.

The posterior carotid foramen remains membranous throughout ontogeny. In the adult the point of entry of the internal carotid into the tympanic cavity is marked by a deep incisure lying between the RTPP and the medial section of the CTPP (fig. VI-1).

An alicochlear commissure is present in young stages of E. europaeus and thus a foramen caroticum primitivum is formed (see also FAWCETT 1918).

In the adult, the anterior carotid foramen does not lie in the petrosphenoid suture (cf. E. rozeti, fig. V-2), but instead pierces the epitympanic wing of the sphenoid (fig. VI-1). GREGORY (1920:173) identifies the foramen of exist of the promontorial artery as the canalis caroticus basisphenoidei. Although the anterior carotid foramen probably does lie close to the original anatomical division between the basisphenoid and alisphenoid, no suture exists between the two elements in the adult.

Ontogenetically, the epitympanic wing of the sphenoid obviously grows completely around the promontorial artery during the closure of the piriform fenestra, thus isolating it from the future petrosphenoid suture. The anterior carotid foramen leads into a short canal which opens into the cranial cavity lateral to the hypophysis.

The foramen of exit of the ramus inferior (foramen caroticum alisphenoidei of GREGORY 1920) is not always present in adult _E. europaeus_. In the adult specimen figured in fig. VI-1, for example, the tympanic process of the alisphenoid does not completely encircle the ramus inferior at its point of exit.

Finally, it should be noted that conditions in _Erinaceus_ are not representative of all Erinaceidae. RICH and RICH (1971) point out that some of the tympanic branchings of the internal carotid are partly enclosed by bony tubes in _Paraechinus aethiopicus_.

6.4.3 NERVES

The routes of major nerves are typical (see fig. I-4); foramina are illustrated in fig. VI-1. Routes and relations are based mainly on conditions in the young infant (MPIH 1966/146).

(1) Facial (VII) Nerve

In the adult the nerve emerges into the middle ear through a complete foramen faciale, but it is otherwise unenclosed for its entire route. During its transit through the tympanic cavity it is in close relation with the proximal stapedial artery (which shares its deep sulcus) and the belly of the stapedius muscle.

In some adults the lateral section of the CTPP meets the tympanohyal, producing a large aperture which accommodates both the facial nerve and the stapedius muscle. This aperture may be regarded as an incipient foramen stylomastoideum definitivum. However, this is a variable feature (the CTPP does not meet the tympanohyal in the specimen illustrated in fig. VI-1).

(2) Chorda Tympani

The chorda tympani is released by the facial nerve distal to the foramen stylomastoideum. It travels around Reichert's cartilage and enters the tympanic cavity through a membranous foramen in front of the apex of the posterior crus (i.e., through the flaccid portion of the tympanic membrane). From here it passes across the medial side of the malleus, penetrates the gonial, and leaves the tympanic cavity through another membranous foramen in the fibrous membrane.

BONDY (1907:309) states that a caudal Chordaforsatz is formed in *E. europaeus*. In the adult this structure is apparently represented by the crest on the tegmen tympani which separates the epitympanic recess from the accessory space in the mastoid eminence.

According to WASSIF (1948:184) the caudal Chordafortsatz is absent in *Hemiechinus auritus* and *Paraeichinus dorsalis*.

(3) Internal Carotid Nerve and Deep Petrosal

The internal carotid nerve divides into two major branches upon leaving the cranial cervical ganglion and ascends the side of the internal carotid artery. It penetrates the fibrous membrane of the tympanic cavity in association with that artery, then follows the promontorial artery to the anterior pole of the promontory. Most of its fibers (as the deep petrosal) follow the greater petrosal out of the tympanic cavity to the pterygoid canal, although a small branch follows the promontorial artery into the cranial cavity.

The internal carotid nerve exchanges fibers with the tympanic nerve along its route, forming an extensive tympanic plexus.

(4) Greater Petrosal

The nerve arises from the geniculate ganglion and almost immediately penetrates the roof of the tympanic cavity, where it associates with the deep petrosal.

In the adult, its foramen of entry is the large aperture in the petrosphenoid suture medial to the sulcus for the ranus inferior. Actually, this foramen is much larger than the nerve itself and represents a remnant of the piriform fenestra which is never completely closed. It is therefore appropriate to term this aperture a persistent piriform fenestra (cf. conditions in soricomorphs, section 7.4.3).

(5) Nerves of the Pterygoid Canal

The deep petrosal and the greater petrosal are the nerves of the pterygoid canal. Together, these nerves accompany the minute artery of the pterygoid canal into the tube visible in the anteromedial extremity of the roof of the middle ear. The pterygoid canal marks the anatomical boundary between the pterygoid and the sphenoid.

(6) Auricular Ramus of the Vagus

This nerve arises from the ganglion of the X nerve as the latter emerges from the posterior lacerate foramen. In young stages, the ramus follows a straight course from its origin across the posterior part of the auditory capsule, enters the stapedius fossa and joins the VII nerve distal to the foramen stylomastoideum primitivum. Its route is entirely extratympanic.

SABAN (1956-57:60) states that in adult *E. europaeus* the ramus passes through a bony canal (*ostium introitum* or mastoid canaliculus) on its way to the VII nerve. I could not identify this canal in my adult specimens, and it is evidently a variable feature. The canal, when it exists, probably passes through the lateral section of the CTPP.

(7) Tympanic Nerve and Lesser Petrosal

The tympanic nerve arises from the IX nerve close to the origin of the ramus auricularis vagi from the X nerve. However, their association is less intimate than in *T. glis* and *E. fuscipes*.

The tympanic nerve swings anteriorly from its origin and passes into D_3 through the large gap between the two sections of the CTPP. It then courses over the medial wall of the apertura fossulae fenestrae cochleae, the stapedial artery, and the fossa for the tensor tympani, where it receives a large contribution from the geniculate ganglion through a foramen in the tegmen tympani.

Continuing forwards as the lesser petrosal, the nerve enters the deep sulcus for the ramus inferior and travels out of the tympanic cavity. It meets the otic ganglion beneath the foramen ovale.

A variation in the route of the tympanic nerve occurs on the left side of MPIH 1966/146. The nerve joined the internal carotid nerve near the point of bifurcation of the internal carotid artery, then re-emerged medial to the tensor tympani fossa. On the right side, the nerve maintained its independence, but was nonetheless in close contact with the internal carotid nerve by means of numerous interconnexions representing the tympanic plexus.

6.5 SUMMARY OF PRINCIPAL FINDINGS

(1) The fibrous membrane of the tympanic cavity forms a small part of the ventral wall in the adult stage, since tympanic processes do not form a complete bulla in modern Erinaceidae.

(2) The bony ventral wall is mostly composed by the tympanic process of the basisphenoid, although small outgrowths from the alisphenoid (and pterygoid), squamosal and petrosal also participate. Both the caudal and rostral tympanic processes of the petrosal are

present, although the latter is very small in modern hedgehogs. The entotympanics are absent.

(3) The ectotympanic is slightly broadened to the lateral in the adult, and is applied (but not fused) to the lateral margin of the tympanic process of the basisphenoid. The apices of the crura are only weakly joined to the roof of the tympanic cavity.

(4) The interface between the tympanic process of the basisphenoid and ectotympanic does not display sutural tissues in the stages examined, and the relationship of the two bone territories is never particularly intimate (semiphaneric condition in adult).

(5) The dorsal wall is mainly formed by the sphenoid. Contributions from the squamosal and petrosal are small (including the tegmen tympani).

(6) The piriform fenestra is closed over in the adult except for the small gap represented by the petrosphenoid suture.

(7) Pneumatization is negligible in its architectural effects, and all accessory cavities are small. Some excavation of the mastoid eminence occurs, although not in the position where one normally finds the mastoid cavity.

(8) The origin of the stapedius muscle lies outside the tympanic cavity throughout ontogeny. A ramus posterior of the stapedial artery, previously unreported for erinaceomorphs, exists in fetal stages. It may involute in postnatal life, however. Routes of nerves are typical.

CHAPTER SEVEN

SORICOMORPHA

METHOD OF DESCRIPTION

7.1 VENTRAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

- 7.1.1 Fibrous Membrane of the Tympanic Cavity
- 7.1.2 Cartilage of the Auditory Tube
- 7.1.3 Tympanic Processes of the Petrosal
- 7.1.4 Ectotympanic
- 7.1.5 Tympanic Process of the Basisphenoid
- 7.1.6 Relationship of the Ectotympanic, Tympanic Process of the Basisphenoid, and Caudal Tympanic Process of the Petrosal
- 7.1.7 Other Tympanic Processes

7.2 DORSAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

- 7.2.1 Tegmen Tympani, Epitympanic Wing of the Petrosal, and Reichert's Cartilage
- 7.2.2 Epitympanic Wing of the Sphenoid
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7.3 PRINCIPAL SPACES AND SEPTA OF THE MIDDLE EAR

7.4 MUSCLES, ARTERIES AND NERVES OF THE MIDDLE EAR

- 7.4.1 Ossicular Muscles
- 7.4.2 Arteries
- 7.4.3 Nerves

7.5 SUMMARY OF PRINCIPAL FINDINGS

7.1 VENTRAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

As in Erinaceomorpha, there is considerable variability in the completeness of bony ventral wall in soricomorphs. In Soricidae, only the caudal tympanic process of the petrosal can be considered relatively large, although there are small ridges developed from the sphenoid and entoglenoid region of the squamosal which bound the fore part of the tympanic cavity. In Solenodon the latter ridges are better developed. In both families the tympanic process of the basisphenoid is absent or vestigial. Tenrecids usually possess a moderately well-developed tympanic process of the basisphenoid (in addition to the other outgrowths mentioned above), while in chrysochlorids the same process forms a complete bulla of relatively large dimensions.

7.1.1 FIBROUS MEMBRANE OF THE TYMPANIC

The fibrous membrane of the tympanic cavity is present in all specimens. The Gabe, Klüver-Barrera and Delafield methods do not adequately contrast different types of connective tissues, and thus the membrane is rather indistinct in most of the figures.

In the specimens of H. semispinosus, the membrane extends from the medial surfaces of the tympanic wing of the basisphenoid to the lateral aspect of the head, beneath the plane of the ectotympanic and the tissues of the presumptive membranous meatus. It is not especially thick in any of the specimens, although it is easily

Table 7-1

SORICOMORPHA

SPECIMENS	No.	CRL[1]	HL[2]	ST[3]	PS[4]	STAINS
TENRECIDAE						
Tenrecinae						
Hemicentetes semispinosus						
I. Fetus	MPIH 1964/84	27.5	16.0	10	cross	Klüver-Barrera, Delafield, Gabe
II. Near-Term Fetus	MPIH 1964/45	40.0	23.0	10	cross	Klüver-Barrera, Delafield, Azan
III. Near-Term Fetus	MPIH 1964/86	42.5	25.0	10	cross	Klüver-Barrera
Setifer setosus						
IV. Fetus	MPIH 1964/93	52.0	24.0	10	cross	Klüver-Barrera
Oryzorictinae						
Microgale dobsoni						
V. Fetus	MPIH 1964/103	31.0	15.0	10	cross	Klüver-Barrera, Gabe
SOLENODONTIDAE						
Solenodon sp.						
VII. Juvenile	MPIH 6863	123.0	87.0	15	cross	Azan, PAS-AB

[1] Crown-rump length (in mm)

[2] Head Length (in mm)

[3] Section thickness (in mμ)

[4] Plane of sectioning.

.....continued

Table 7-1 -- Continued

NOTES ON SPECIMENS

The suborder Soricomorpha, as defined by MCDOWELL (1958), includes four rather divergent families (Tenrecidae[1], Chrysochloridae, Solenodontidae, and Soricidae). Unfortunately, the range of suitable sectioned material available to me was restricted to several tenrecs and a single solenodon.

The tenrecs were procured from gravid females captured in Madagascar by Dr. H. STEPHAN (Neurobiologische Abteilung, MPIH). Specimen II (MPIH 1964/45) is listed in the catalogue as a neonate. However, it was probably a near-term fetus which was aborted when its mother was captured, for a larger specimen (MPIH 1964/86) was still *in utero* when collected.

The solenodon (MPIH 6863) is definitely postnatal and is listed in the table as a juvenile (see also frontispiece)[2]. Dr. STEPHAN, who kindly provided this specimen, was unable to give me its history. Since two species of *Solenodon* are currently recognized (the agouta of Hispaniola, *S. paradoxus*; the almique of Cuba, *S. cubanus*), I have denoted it as *Solenodon* sp. in the table.

Dr. STEPHAN permitted me to study his personal collection of macerated skulls of adult tenrecs, which included specimens of *Hemicentetes semispinosus*, *Setifer setosus*, *Tenrec ecaudatus*, *Microgale (Nesogale) dobsoni*, *Microgale (Nesogale) talazaci* and *Potamogale velox*. Regrettably, no adult specimen of *Solenodon* was available.

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[1] The so-called otter shrews are sometimes allocated to their own family (Potamogalidae).

[2] Adult specimens range between 280-325 mm CRL (WALKER *et al*., 1964:104).

discerned in the Azan series of MPIH 1964/45 (e.g., fig. VII-11b).

Posteriorly, the fibrous membrane isolates the rear of the cavum tympani (saccus posterior), the apertura fossulae fenestrae cochleae and the adjoining diverticulum D_3 from ventrally situated soft tissues like the digastric muscle (fig. VII-17). The facial nerve and the tendon of the stapedius muscle penetrate the membrane where it fills the gap between the tympanohyal and lateral section of the CTPP (fig. VII-16). The internal carotid artery (fig. VII-7a,b,c), the auditory tube and other structures enter the tympanic cavity through apertures within the fibrous membrane.

The fetuses of S. setotsus (MPIH 1964/93) and M. dobsoni (MPIH 1964/103) are very similar to the specimens of H. semispinosus for this feature and do not require separate description.

The relationship of the fibrous membrane to the tympanic process of the basisphenoid is identical in tenrecs and Erinaceus (see 6.1.1.1).

The fibrous membrane of the Solenodon juvenile (MPIH 6863) is probably close to its definitive condition. It has the character of dense connective tissue, and the thick feltwork of large bundles of fibers is quite evident (fig. VII-33). The tissue is well-vascularized and exhibits no peculiarities.

The ventral surface of the fibrous membrane joins the sheets of connective tissue interposed between or covering the muscles, nerves and blood vessels situated beneath the basicranium. The dorsal (or tympanic) surface is in direct contact with the definitive mucosal lining of the tympanic cavity, since the mucoid tissue which originally filled most of the presumptive middle ear has been resorbed (fig. VII-32). Laterally, the fibrous membrane is tightly bound to the periosteum of the ectotympanic, as in fetal tenrecs and most other mammals investigated here. Further laterally, the membrane blends with the tissues contributing to the membranous meatus.

7.1.2 CARTILAGE OF THE AUDITORY TUBE

Young tenrecs are similar to young elephant shrews and hedgehogs in the subtriangular form and transverse orientation of the cartilage of the tube. The auditory tube is short and resides in the deep trough produced by the ventral reflection of the anterior margin of the cartilage (fig. VII-26). The cartilage of the tube is accommodated in the interval between the medial end of the tympanic processes of the alisphenoid and the basisphenoid. In the adult, there is a prominent gutter in this location (figs. VII-1, VII-2).

The cartilage of the tube displays no unusual features, other than the fact that it is still in fairly young cartilage even in the older fetuses. There are no accessory cartilages associated with it, and it ends precisely where the auditory tube opens into the cavum tympani.

In the specimen of Solenodon sp., the tubal cartilage is vertically positioned and staff-shaped in cross-section (fig. VII-31). There is nothing in its form and relations which would indicate that an entotympanic element is present.

7.1.3 TYMPANIC PROCESSES OF THE PETROSAL

7.1.3.1 Introduction

Available specimens and published descriptions indicate that the two central subfamilies of Tenrecidae exhibit a consistent, if minor, difference in the style of petrosal participation in the ventral wall of the tympanic cavity. In Oryzorictinae (figs. VII-1, VII-3), the CTPP is large and completely obscures the apertura fossulae fenestrae cochleae; also, its free anterior margin broadly contacts the posterior crus of the ectotympanic. In Tenrecinae (figs. VII-2, VII-3), on the other hand, the CTPP is always small and thus covers only a limited portion of the apertura; further, it never articulates with the posterior crus of the ectotympanic (athictic condition).

Another difference may lie with a low rampart on the ventral surface of the promontory, which I have seen only in adult oryzorictines (fig. VII-1). This rampart is continuous with the medial side of the CTPP and runs to the anterior pole of the promontory. Its positioning is similar to that of the RTPP encountered in young strepsirhines and elephant shrews, but its small size recalls the crista petrosi of tree shrews (fig. IV-4). However, since it is not associated with an entotympanic bulla, I prefer to regard it as a true tympanic process of the petrosal (i.e., a RTPP). MCDOWELL's (1958:189, fig. 37; see fig. VII-3) figures of adult tenrecid auditory regions do not adequately differentiate between the RTPP and the projecting medial wall of the promontory (cf. fig. VII-1), which gives a misleading impression of the actual size of the process.

The RTPP is apparently completely absent in tenrecines.

In the third subfamily, Potamagalinae, the CTPP is small in *Potamogale*, but relatively larger in *Micropotamogale*. According to GUTH, HEIM de BALSAC and LAMOTTE (1959), the CTPP actually contacts the posterior crus of the ectotympanic, under cover of the projecting tympanohyal.

Solenodon exhibits a large CTPP. It is normally fused, in the adult, with the posterior crus of the ectotympanic (MCDOWELL 1958; see also 7.1.6).

The sectioned specimens establish that the development of the CTPP is essentially the same in both Tenrecinae and Oryzorictinae, despite adult differences in size. Furthermore, the pattern of development is highly similar to that of *E. europaeus* (see 6.1.3). Specifically, the CTPP arises from the areas adjacent to and including the medial and lateral sidewalls of the apertura fossulae fenestrae cochleae. As in all non-strepsirhines investigated here, the posterior continuation of the crista parotica does not take part in the formation of the CTPP. Accordingly, the origin of the stapedius is extratympanic.

Conditions in adult specimens of *P. velox* suggest that the CTPP develops as in tenrecs.

The CTPP of *Solenodon* is identical to tenrecs and erinaceids in respect of its sites of origin.

7.1.3.2 Development of the Processus Recessus

It has not been previously reported that the processus recessus has a bipartite origin in some (if not all) tenrecs (cf. LEIMGRUBER

1939; ROUX 1947). Since this structure is involved in the production of the CTPP, it is useful to provide an account of its development and to re-interpret certain features of ROUX' (1947) analysis of its ontogeny.

In describing the auditory capsule of a 20.4 mm CRL specimen of _S. setosus_, ROUX (1947:337) mentioned that the processus recessus was 'primitive' since it was merely a short projection of the cochlear floor which did not reach the anteroventral surface of the pars canalicularis. Thus, the recessus scalae tympani remained partly extracapsular and the medial and lateral apertures were incomplete.

However, he noted (1947:339) for a much older specimen (47.4 mm CRL) that, in addition to the 'primitive' processus recessus, there was

> ...a slender cartilaginous spur..., extending backwards and medially from the lower lateral surface of the pars canalicularis in front to the postero-lateral edge of the processus recessus behind. This cartilage spur isolates a fenestra rotunda laterally but does not render the recessus scalae tympani intracapsular as yet. Neither does it delimit the apertura medialis ...from the foramen jugulare.

The feature that ROUX describes as a "cartilaginous spur" is actually a part of the CTPP (specifically, the lateral section). As he notes, it does not fulfill the function of a processus recessus in terms of enclosing the recessus scalae tympani or delimiting its aperturae.

Unknown to ROUX, another cartilaginous process develops beneath the recessus scalae tympani; it can be discerned in the 52 mm CRL stage of S. setosus (MPIH 1964/93). It arises from the anteroventral surface of pars canalicularis (near the posterior root of the lateral section of the CTPP) and juts forward to rest on ROUX' 'primitive' processus recessus. Unfortunately, the process is hard to discern in the figures (figs. VII-25b,c) because Kluver-Barrera does not adequately visualize young cartilage. However, precisely the same conditions obtain in the two older specimens of H. semispinosus (figs. VII-18a,b,c), with the difference that this outgrowth is now mostly ossified.

Since this outgrowth completes the floor of the recessus scalae tympani, it is proper to refer to it as the processus recessus posterior, and to ROUX' 'primitive' processus recessus as the processus recessus anterior. A bipartite processus recessus is not common, but it has been found in some other mammals (notably Homo; cf. REINBACH 1963). During its later growth and development, the processus recessus forms all there is of the small medial section of the CTPP in Tenrecinae (fig. VII-2).

Why ROUX (1947) did not regard his "cartilaginous spur" as part of a CTPP is unclear, since it has nearly the same relations (if not the size) of the CTPP he described for young stages of Suncus orangiae. He may have been influenced by adult conditions, for the CTPP is exceptionally small in Setifer in all stages of ontogeny (fig. VII-3).

7.1.3.3 Structure, Relations and Development of the Caudal Tympanic Process

(1) Conditions in Specimens of *Hemicentetes semispinosus* and *Setifer setosus*

The development of the CTPP is essentially identical in Tenrecinae and *E. europaeus* (see 6.1.3) and requires only brief description. It is not possible to distinguish a posterior section in any useful way, and thus the CTPP is divided only into medial and lateral sections.

The lateral section is a low ridge of cartilage in the youngest specimen of *H. semispinosus* (MPIH 1964/84). The ridge is prominent only in its posterior part, where it extends from the anteroventral surface of the pars canalicularis (fig. VII-8c). The processus recessus anterior is present, but the processus recessus posterior is not yet represented (fig. VII-8c).

In MPIH 1964/45 and MPIH 1964/86, the posterior part of the pars cochlearis and the anteroventral part of the pars canalicularis are almost completely ossified. The lateral section of the CTPP (which is also bony) can now be traced from a position beneath the apertura fenestrae ovalis (fig. VII-15) to the pars canalicularis, where it is confluent with the root of the processus recessus posterior (fig. VII-18).

Although it is not evident in these specimens, it is obvious from the adult state (fig. VII-3) that the medial section of the CTPP forms as a small lateral prolongation of the processus recessus posterior.

In the adult, the CTPP has relations which are virtually identical to those of the late fetus. The two sections of the CTPP are coalesced behind the apertura fossulae fenestrae cochleae and diverticulum D_3, but only partially cover them. The lateral section of the CTPP is in close relation to Reichert's cartilage in the fetus (e.g., fig. VII-15), and the two usually meet in the adult (fig. VII-2).

S. setosus MPIH 1964/43 does not depart in any significant way from the two older specimens of _H. semispinosus_. The lateral section of the CTPP forms first, as in the streaked tenrec, and has similar relations to the rest of the auditory capsule (fig. VII-25). The processus recessus posterior is present and still completely cartilaginous.

In the adult _S. setosus_ the CTPP is so small that it is hardly recognizable (fig. VII-3). Evidently, it grows very little during postnatal life. The process retains a distinctly bilobate appearance, the lobes corresponding to the medial and lateral sections of the fetal CTPP. Contact with the tympanohyal is variable.

(2) Conditions in _Microgale dobsoni_ MPIH 1964/103

In the sectioned specimen (MPIH 1964/103) the CTPP is a massive outgrowth arising from both sidewalls of the apertura fossulae fenestrae cochleae and the adjacent part of the anteroventral floor of the pars canalicularis (figs. 30a,b,c,d). Whether the processus recessus is bipartite in this species cannot be determined on the basis of this specimen, as ossification is too far advanced. It is not meaningful to subdivide this outgrowth into medial and lateral sections, for it presents no structural divisions of that sort.

On the other hand, it is quite obvious that the CTPP of the long-tailed tenrec is only a much larger version of that of the streaked tenrec (cf. figs. VII-18 and VII-30).

Although the sectioned specimen is prenatal, the CTPP already completely covers the apertura fossulae fenestrae cochleae. Evidently the cartilaginous CTPP must have been quite extensive, for small islands of cartilage are still present in the otherwise ossified anterior margin (fig. VII-30b). The CTPP doubtless arises from the auditory capsule, as in other tenrecs, and does not have a separate existence at any stage of ontogeny.

The low ridge provisionally identified as the RTPP in the adult stage (see 7.1.3.1 and fig. VII-1) may be represented by the tiny row of trabeculae anterior to the margin of the apertura fossulae fenestrae cochleae (fig. VII-30a). At the stage represented by MPIH 1964/103, however, the trabeculae do not run along the entire length of the ventral surface of the promontory, for the anterior pole of the latter is still cartilaginous (fig. VII-29).

In the adult, the CTPP articulates with the posterior crus of the ectotympanic and the tympanohyal (these articulations are not found in the fetus). However, it undergoes only a small degree of inflation, for its relations are otherwise like those of MPIH 1964/103. The RTPP(?) extends from the entire length of the ventral surface of the promontory and meets the posterior margin of the tympanic process of the basisphenoid (fig. VII-1). It does not, however, contact the ectotympanic.

(3) Conditions in Solenodon sp.
MPIH 6863

The CTPP of this specimen is entirely bony, so little can be reported concerning its ontogeny. However, its relations are typical: as in tenrecs, it arises from the sidewalls of the apertura fossulae fenestrae cochleae and the adjacent part of the anteroventral floor of the pars canalicularis (fig. VII-36). Its free anterior margin is exceptionally rugose and in the process of fusing with the posterior crus of the ectotympanic (fig. VII-34).

A RTPP is not represented in the sectioned specimen and appears to be absent in the adult (cf. figs. in MCDOWELL 1958; GREGORY 1910; ALLEN 1908).

The CTPP does not contact the tympanohyal in the adult (MCDOWELL 1958:139), although the interval between them is very small.

7.1.4 ECTOTYMPANIC

7.1.4.1 Structure, Relations and Development

The ectotympanic retains a horseshoe-shape throughout ontogeny in Tenrecidae. It is slightly broadened to the lateral in the adult, although not to the extent seen in Erinaceinae (cf. fig. VI-2 and fig. VII-1). The sectioned and macerated specimens indicate that there is little structural variability in this element among tenrecs.

In young stages the ectotympanic is freely suspended in the ventral wall by means of connective tissue (fibrous membrane of the tympanic cavity, pars flaccida of the tympanic membrane). The apex of the anterior crus is considerably broadened and bears a prominent malleolar sulcus for the gonial and Meckel's cartilage (fig. VII-10). The posterior crus of the ectotympanic ends in a fine spit and is inserted between the root of Reichert's cartilage and the auditory capsule, as usual.

In adult tenrecines, conditions are essentially identical to those found in the late fetus. The ectotympanic evidently grows a small amount during postnatal life, and lies in close proximity to the tympanic process of the alisphenoid, entoglenoid process of the squamosal, tympanic process of the basisphenoid, and the tympanohyal. However, it is not fused to any of them. In oryzorictines, the ectotympanic receives additional bony support from the CTPP, but the suture between them remains open. Although the elements producing the bony ventral wall of the tympanic cavity are in intimate relation with the ectotympanic in Potamogalinae as well, the latter does not fuse with them either (fig. VII-3).

The gonial apparently does not fuse with the ectotympanic at any ontogenetic stage.

MCDOWELL's (1958:139) fig. 5d seems to imply that the ectotympanic in the adult Solenodon is broadened medially as well as laterally. Medial broadening, however, is not evident in the sectioned juvenile (fig. VII-33). Another difference from tenrecs is a small but definite anterior process.

As in young Erinaceus (see 6.1.4), the ectotympanic consists of young woven bone rather than 'intermediate' bone.

7.1.4.2 Inclination of the Ectotympanic

The ectotympanic undergoes only a small amount of rotation during ontogeny in Tenrecidae (see table 7-2). In the absence of other specimens, it is difficult to explain why the juvenile specimen of Solenodon possesses so high an inclination value (40°). The only tympanic process which could exert any influence on the position of the ectotympanic in this case is the CTPP, but from its position one would think that it would affect only the declination of the ectotympanic, not its inclination. Solenodon is a clear exception to the general rule that the ectotympanic is only slightly inclined in insectivores.

I was unable to find published inclination values for adult tenrecs and solenodons, although there is little reason to suppose that they would differ greatly from those found in young specimens. HENSON (1961) records a value of 23° for adult specimens of the soricid species Cryptotis parva.

7.1.5 TYMPANIC PROCESS OF THE BASISPHENOID

7.1.5.1 Introduction

The tenrecoid and soricoid divisions of Soricomorpha markedly differ in the degree of basisphenoidal participation in the ventral wall of the tympanic cavity. In Tenrecidea (Tenrecidae and Chrysochloridae),

Table 7-2

INCLINATION OF THE ECTOTYMPANIC IN YOUNG SORICOMORPHA

Specimen No.	Angle of Inclination		Average Inclination
	L	R	
Hemicentetes semispinosus			
MPIH 1964/84	19°	21°	20.0°
MPIH 1964/45	19°	20°	19.5°
MPIH 1964/86	28°	26°	27.0°
Setifer setosus			
MPIH 1964/93	26°	26°	26.0°
Microgale dobsoni			
MPIH 1964/103	24°	22°	23.0°
Solenodon sp.			
MPIH 6863	40°	40°	40.0°

For computation of the angle of inclination, see note accompanying table 2-2.

the tympanic process of the basisphenoid is well-developed, as in other lipotyphlans. In Soricoidea (Soricidae and Solenodontidae) the tympanic process is absent or nearly so. It may be mentioned that the same contrast existed in the old concept of Soricoidea, which placed soricids and talpids in close proximity (tympanic process of the basisphenoid well-developed in latter).

The tympanic process of adult tenrecids (fig. VII-3) is quite similar to that of erinaceids (fig. VI-1). Trapezoidal in form, it descends from the body of the basisphenoid to cover a small portion of the medial part of the ectotympanic.

There are some minor subfamilial differences in the size and relations of the tympanic process of the basisphenoid to other elements of the auditory region. In Potamogalidae (fig. VII-3), the anterior end of the process contacts the large entoglenoid process of the squamosal and thus defines a large aperture (through which both the auditory tube and the ramus inferior pass). In other tenrecs, there is only a more-or-less well-defined gutter for the auditory tube. In Tenrecinae the tympanic process flares posteriorly beyond the level of the basisphenoid-basioccipital synchondrosis and overlaps part of the ventromedial side of the promontory (cf. *E. europaeus*, fig. VI-1). In Oryzorictinae, the process terminates at this suture instead of continuing beneath the promontory (although it does contact the extreme anterior end of the ridge earlier identified as a possible RTPP). In Potamogalidae the tympanic process of the basisphenoid is exceptionally long and actually meets the leading edge of the CTPP at the site of the posterior carotid foramen.

7.1.5.2 Development of the Tympanic Process of the Basisphenoid in *H. semispinosus* and *S. setosus*

As others have noted (e.g., VAN KAMPEN 1905:451-452; VAN DER KLAAUW 1929:546), PARKER's (1886) view that the tympanic process of the basisphenoid is an 'os bullae' (entotympanic) which has secondarily lost its independence cannot be supported. It is quite clear from ROUX' (1947) investigations and the specimens described here that the tympanic process is an intramembranous excrescence of the basisphenoid and shows no sign of having had an independent existence.

The tympanic process is present in the youngest specimen of *H. semispinosus* (MPIH 1964/84). At this stage it is limited to the area just behind the position of the lumen of the auditory tube (fig. VII-6).

The process evidently keeps pace with the expansion of the basisphenoid center in the central stem. In the two older specimens (MPIH 1964/45 and MPIH 1964/45) it arises from the entire length of basisphenoid element (figs. VII-10 to VII-13).

The Azan series of MPIH 1964/45 permits a determination of the relationship of the fibrous membrane of the tympanic cavity to the tympanic process of the basisphenoid. As may be seen in fig. VII-11b, the growing ventral margin of the process is not enclosed within the membrane, which is instead applied against its surface. Although the ventral margin is actively growing judging from the thick palisade of osteoblasts surrounding it, the tympanic process does not exhibit any sign of secondary cartilage.

The posterior end of the pterygoid has already fused to the basisphenoid in the youngest specimen, and accordingly it is not possible to determine its relationship to the tympanic wing of the basisphenoid (see however 7.1.5.3). The pterygoid canal is useless as a guide to the original boundary between the two elements because its posterior orifice lies farther back than usual, well within the epitympanic wing of the alisphenoid (fig. VII-10). However, it is likely that the pterygoid terminates in front of the gutter for the auditory tube and thus makes no contribution to the tympanic process of the basisphenoid.

A similar problem accompanies the evaluation of the tympanic process of the basisphenoid in the sectioned specimen of S. setosus (MPIH 1964/93). It is clear from ROUX' (1947) descriptions of earlier stages that the posterior part of the pterygoid is massive. However, at the 52.0 mm CRL stage the end of the pterygoid and the basisphenoid are fused in such a way that it is not possible to make a structural division between them. In serial sections, material which must be pterygoidal in origin is continuous with the enormous tympanic process of the basisphenoid. However, judging from ROUX' (1947:341) fig. 61C, the posterior end of the pterygoid probably terminates just in front of or just above the position of the auditory tube and its associated gutter (figs. VII-19 to VII-22).

The relationship of the tympanic process and the fibrous membrane of the tympanic cavity appears to be identical to that encountered in H. semispinosus, although this is difficult to judge with Klüver-Barrera staining (figs. VII-23, VII-24).

7.1.5.3 Development of the Tympanic Process of the Basisphenoid in M. dobsoni

The single fetal specimen of M. dobsoni (MPIH 1964/103) does not differ from the specimens of H. semispinosus except in one important detail. Even though ossification is well-advanced in this specimen, the posterior end of the pterygoid is still free (fig. VII-26). Unlike S. setosus MPIH 1964/93, this portion of the pterygoid is merely a small, flat plate which terminates medial to the position of the cartilage of the tube and the posterior rim of the foramen ovale in cross-sections. The tympanic process of the basisphenoid begins posterior to this level (fig. VII-28) and thus does not contain any pterygoidal material.

7.1.5.4 Conditions in Solenodon sp. MPIH 6863

MCDOWELL (1958:142) believes that Solenodon possesses a vestigial tympanic process of the basisphenoid in the form of a low, blunt ridge medial to the tympanic end of the vidian canal.

I am not sure that this ridge is present in the sectioned juvenile; it may be the small elevation adjacent to the cartilage of the tube in fig. VII-31. However, its position and relation to the pterygoid canal indicates that this elevation may be formed from pterygoidal material.

7.1.6 RELATIONSHIP OF THE ECTOTYMPANIC, TYMPANIC PROCESS OF THE BASISPHENOID AND CAUDAL TYMPANIC PROCESS OF THE PETROSAL

The ventral margin of the tympanic process of the basisphenoid partly occuldes the medial side of the body of the ectotympanic in all adult tenrecs I have seen (cf. figs. VII-1, VII-2, VII-3). The degree to which it covers the ectotympanic varies, but it is never complete and is not accompanied by synostotic union. The Potamogalidae appear to display the greatest amount of basiphenoidal overgrowth (see GUTH, HEIM de BALSAC and LAMOTTE 1959; fig. VII-3).

In all sectioned specimens the ventral margin of the basisphenoid still lies a distance above the rim of the ectotympanic (d.g., figs. VII-11, VII-23). The two are, however, in communication by means of the fibrous membrane of the tympanic cavity. Since the ectotympanic is essentially free (particularly in tenrecines), it is possible that the apparent overgrowth of the basisphenoid exhibited by the adult skulls is an artefact of maceration; shrinkage or removal of the fibrous membrane during the preparation of adults might alter the true anatomical position of the ectotympanic. However, I doubt that this is the case. The ventral margin of the tympanic process of the basisphenoid is still actively growing in late fetal stages, and presumably comes into closer proximity to the ectotympanic postnatally. Also, adult skulls are quite consistent in the observed ectotympanic-tympanic process of the basisphenoid relationship (semiphaneric condition).

As previously noted, the CTPP contacts the posterior crus of the ectotympanic in Oryzorictinae and Micropotamogale (7.1.3.1). However, the two are not yet in close contact in M. dobsoni MPIH 1964/103, and a complete array of sutural tissues has not differentiated. Instead, the ectotympanic is bound to the CTPP by the fibrous membrane of the tympanic cavity alone.

The CTPP completely fuses with the posterior crus of the ectotympanic in Solenodon. In the sectioned specimen (MPIH 6863), the suture separating the two is in the process of obliteration. Within the richly-vascularized sutural tissues, a transitory tissue has differentiated which is similar to that found in the ectotympanic-petrosal plate suture of G. senegalensis MPIH 1967/117 (cf. figs. III-9 and VII-34).

7.1.7 OTHER TYMPANIC PROCESSES

7.1.7.1 Tympanic Process of the Alisphenoid

The tympanic process of the alisphenoid varies in size from small in H. semispinosus (fig. VII-2) to large in S. setosus and T. ecaudatus (fig. VII-3). In all cases, it is a continuous rampart which runs from the gutter for the auditory tube to the lateral margin of the entoglenoid process of the squamosal, behind the posterior rim of foramen ovale. As in E. europaeus, there is evidence for pterygoidal participation in the angle where the tympanic process of the alisphenoid becomes confluent with the tympanic process of the basisphenoid.

The foramen for the ramus inferior (when present) passes through the lateral part of the process, or through the suture between the latter and the entoglenoid process of the squamosal. This foramen also accommodates the lesser petrosal nerve. In species lacking the ramus inferior (e.g., H. semispinosus), a small foramen may be found in the same location. However, in such cases the aperture accommodates the lesser petrosal nerve alone.

Because of its transverse orientation, the youthful condition of the tympanic process of the alisphenoid is difficult to visualize from cross-sections. Its large size in S. setosus MPIH 1964/93, however, permits an adequate description of its relations.

Figs. VII-19, VII-20 and VII-21 illustrate sections through the process at different transverse levels. Fig. VII-19 passes through the posterior rim of foramen ovale and the lumen of the auditory tube. It depicts the anteromedial part of the process, which is the large mass of bone beneath the nerves of the pterygoid canal. The pterygoid bone must make some contribution to this part of the process, although it cannot be discriminated from the basisphenoid and alisphenoid at this stage of development.

Fig. VII-20 depicts conditions directly behind the tympanic aperture of the auditory tube. The pterygoid is probably no longer represented at this level, and the large descending process seen in this section is the true tympanic process of the basisphenoid. The confluence of the tympanic processes of the basisphenoid and alisphenoid is obvious if figs. VII-19 and VII-20 are compared.

Conditions are essentially the same in fig. VII-21; the tympanic processes of the basisphenoid and alisphenoid are easier to separate because a greater distance lies between them at this transverse level.

The tympanic process of the alisphenoid is much smaller in the sectioned specimens of H. semispinosus and M. dobsoni, and consequently its relations are more difficult to depict with serial sections. However, the thickened portions of the alisphenoid adjacent to foramen ovale and the ramus inferior can be discriminated fairly easily in figs. VII-26 and VII-27. The posterior part of the pterygoid undoubtedly makes a small contribution to the process.

LEIMGRUBER (1939:581) found that the pterygoid was bipartite in the 20.0 and 23.5 mm CRL stages of T. ecaudatus. The intramembranous part was situated near the anterior pole of the promontory, at a considerable distance from the cartilaginous part. Judging from his illustrations (p. 567: fig. 16N,O), the intramembranous part is also distantly separated from the processus alaris of the central stem, which is a most uncharacteristic location (cf. DE BEER 1937:435). However, the ossification is presumably correctly identified[1], and it is certainly in a position where it might partake in the future tympanic process of the alisphenoid.

The tympanic process of the alisphenoid of Solenodon is relatively small, but does not differ significantly from that of tenrecs (fig. VII-31). The advanced age of the sectioned specimen makes it impossible to determine whether there is a pterygoidal contribution. MCDOWELL (1958:162) considers the fact that the ramus inferior merely grooves, rather than perforates, the process to be a specific resemblance to soricids.

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[1] It is worth remarking that LEIMGRUBER (1939:578) specifically notes that the ectotympanic bone is missing in his specimens. The position of his 'dermal part of the pterygoid' certainly conforms better to that normally associated with the ectotympanic element.

7.1.7.2 Entoglenoid Process of the Squamosal

MCDOWELL (1958:181) convincingly argues that the process which clasps the mandibular condyle in Soricomorpha is not the equivalent of the postglenoid process of most other mammals, but a modified entoglenoid process. However, inasmuch as the entoglenoid process completes the anterolateral border of the tympanic cavity, it may be regarded as a tympanic process as well.

The entoglenoid process is very well developed in most of the sectioned specimens (figs. VII-10, VII-21). The process articulates medially with the tympanic process of the alisphenoid; in the adult, the two outgrowths are often completely fused, although the original boundary between them may be identified by reference to the foramen for the ramus inferior (see 7.1.7.1).

The entoglenoid process is also large in the sectioned specimen of Solenodon sp. I can confirm MCDOWELL's (1958) belief that the small groove on the posterior face of the process accommodates the chorda tympani (fig. VII-31). This groove is also found in certain tenrecs in the adult stage (fig. VII-3). According to MCDOWELL, the presence of this groove constitutes further evidence that the process is indeed formed by the entoglenoidal part of the squamosal, for the true postglenoid process of most mammals lies lateral or dorsolateral to the path of the chorda tympani.

7.2 DORSAL WALL OF THE MIDDLE EAR AND ASSOCIATED STRUCTURES

The relative contributions of the bones which make up the roof of the tympanic cavity in adult soricoids (figs. VII-1, VII-2) differs considerably from E. europaeus (fig. VI-1). Anteromedially, the roof is formed by the epitympanic wing of the sphenoid. This plate articulates laterally with the relatively enormous epitympanic wing of the squamosal. The tegmen tympani is essentially excluded from the epitympanic recess, which is instead almost entirely covered by the epitympanic wing of the squamosal. The tegmen tympani does, however, cover the posterior crus of the incus. The epitympanic wing of the petrosal occupies a small part of the central portion of the roof.

A persistent piriform fenestra is characteristic of many soricoid species, although it is not universal.

7.2.1 TEGMEN TYMPANI, EPITYMPANIC WING OF THE PETROSAL, AND REICHERT'S CARTILAGE

7.2.1.1 Tenrecidae

The tegmen tympani is extremely short in the adult tenrec (figs. VII-1, VII-2). It is merely a narrow tubercle on the anterolateral side of the pars canalicularis and makes only a small contribution to the roof of the tympanic cavity.

The tegmen tympani evidently completes most of its development in late prenatal life. In the two older specimens of H. semispinosus (MPIH 1964/45 and MPIH 1964/86), the tegmen tympani projects from its origin (fig. VII-15) a short distance between the squamosal laterally and the pars cochlearis medially (fig. VII-14). It terminates at the same transverse level where the ramus superior enters the cranial cavity and the VII nerve enters the tympanic cavity. In the adult stage (fig. VII-2), the tegmen tympani has precisely the same relations, the only difference being that it is completely ossified. The tegmen tympani does not even grow so far anteriorly as to enclose the foramen for the ramus superior, which instead lies in the suture between the tegmen and the large epitympanic wing of the squamosal. The same conditions of little or no postnatal growth characterize S. setosus, M. dobsoni and probably other tenrecids as well (figs. VII-24, VII-29).

In all sectioned specimens the tegmen is cartilaginous, although ossification proceeding from the pars canalicularis is beginning to penetrate its root in H. semispinosus MPIH 1964/45 and MPIH 1964/86 (fig. VII-15).

The posterior continuation of the crista parotica is relatively larger in the specimen of S. setosus (fig. VII-25) than it is in the specimens of H. semispinosus and M. dobsoni (figs. Vii-17, VII-30).

A relatively large epitympanic wing of the petrosal is identifiable in all sectioned specimens. In the H. semispinosus series, it initially arises as a tab-like outgrowth of the cartilaginous dorsolateral wall of the promontory, in advance of the foramen faciale (fig. VII-6). Its chief relation is to the tensor tympani, some fibers of which arise from it. This outgrowth ossifies in continuity with the promontory and increases in size, later coming into relation laterally with the epitympanic wing of the squamosal (fig. VII-13). Since it begins in front of the foramen faciale, it has no primary relationship with the tegmen tympani.

Identical projecting shelves are found in the sectioned specimens of *S. setosus* and *M. dobsoni* (e.g., fig. VII-23). In the former, the epitympanic wing extends from the foramen faciale (fig. VII-24) to the anterior pole of the promontory (fig. VII-22).

A tegminal *Chordaforsatz* is absent in tenrecs.

Characteristic of most tenrecs is a relatively large piriform fenestra persisting into the adult stage. Its development may be traced by reference to fetal and postnatal stages of the streaked tenrec, *H. semispinosus*.

In young stages of *H. semispinosus*, the piriform fenestra is a wide interval between the anterior pole of the promontory and the developing epitympanic wing of the sphenoid. Because of the slight development of the tegmen tympani, the fenestra continues posteriorly as a long, narrow fissure between the epitympanic wing of the petrosal and the epitympanic wing of the squamosal. It may be said to end at the site of the foramen faciale, where it meets the tegmen tympani and the anterolateral part of the pars cochlearis.

The anterior portion of the piriform fenestra persists into the adult stage as a relatively wide aperture, despite the considerable growth of the epitympanic wing of the alisphenoid. The posterior portion of the fenestra is further narrowed by the approximation of the epitympanic wings of the petrosal and squamosal (although the two projections do not normally fuse). The terminal part of the posterior portion also remains open, since it becomes the foramen for the ramus superior.

Similar conditions are found in other tenrecs, although the size of the piriform fenestra varies greatly. In *T. ecaudatus* it is barely indicated, and the bones and processes involved in the bounding of the fenestra are in very close contact. In *M. dobsoni*, the anterior portion remains very large (fig. VII-1), but the posterior portion is almost completely obliterated. There may also be some degree of individual variation in the size of the fenestra in the adult. In adult specimens of *H. semispinosus* that I have seen, it is fairly large. However, it is shown as absent in the specimen illustrated by MCDOWELL (1958:189, fig. 37G).

Reichert's cartilage shows normal relations. The specimen of *M. dobsoni* shows a center for the stylohyal (fig. VII-28), but the cartilage is largely unossified in the other fetuses. In the adult, the tympanohyal is fully exposed on the lateral side of the auditory region, and is in close contact with the lateral side of the CTPP and the posterior crus of the ectotympanic (fig. VII-3). The proximal part of the tympanohyal is partly enclosed by a bony sheath derived from the squamosal (cf. fig. VII-14).

7.2.1.2 Solenodon

The roof of the tympanic cavity in the juvenile specimen (MPIH 6863) does not differ significantly from that of the adult. Accordingly, little need be added to MCDOWELL's (1958) excellent description of adult conditions.

The tegmen tympani is relatively larger than in tenrecs, and takes part in the epitympanic recess to a great extent (fig. VII-32). Whether an epitympanic wing of the petrosal is formed earlier in ontogeny cannot be determined from this specimen, since the tegmen is continuous with the length of the dorsolateral side of the promontory. The most conspicuous feature of the tegmen tympani is a long, steep-walled sulcus which runs for most of its length, and which carries the proximal stapedial and the posterior part of the tensor tympani (fig. VII-32). MCDOWELL (1958:142) believes that a Chordaforsatz is present, but I could not identify one in the juvenile.

Reichert's cartilage is ossified except for a small strip between the tympanohyal and the stylohyal.

7.2.2 EPITYMPANIC WING OF THE SPHENOID

The epitympanic wing of the sphenoid is very large in adult tenrecs (cf. *E. europaeus*, 6.2.2). However, a significant part is covered laterally the epitympanic wing of the squamosal, which is also quite large. Accordingly, the sphenosquamosal suture tends to appear in the middle portion of the roof of the tympanic cavity (figs. VII-1, VII-2). The basisphenoid definitely contributes to the medial part of the epitympanic wing.

The epitympanic wing of the sphenoid is an intramembranous extension of the body of the alisphenoid and the lateral margin of the basisphenoid and presents no peculiarities of development. It is quite short in all of the sectioned specimens and extends only a short distance posterior to the tympanic process of the alisphenoid (cf. figs. VII-21, VII-22). Evidently, the wing goes through its major growth spurt in postnatal life, as VAN KAMPEN (1905:423) has previously noted.

A minor feature of interest appearing in figs. VII-5, VII-9, VII-10 and VII-11 deserves mention. This feature is the tensor veli palatini, the muscle which tenses the soft palate. This muscle normally attaches to the cartilage of the tube surrounding elements (often the tympanic bulla, as in strepsirhines, and sometimes the ectotympanic, as in shrews [GASC 1963]). In _S_. _setosus_ and _M_. _dobsoni_ this muscle attaches to the cartilage of the tube and apparently the region in front of the developing tympanic process of the alisphenoid. In _H_. _semispinosus_, however, the muscle has an exceptionally long insertion which carries over the probable site of the developing tympanic process (fig. VII-10) onto the anterior part of the epitympanic wing of the sphenoid (fig. VII-11). A long insertion for this muscle occurs in some other mammals (e.g., _Procyon lotor_; STORY 1951).

The pterygoid canal begins in the substance of the epitympanic wing of the sphenoid of both fetus and adult (fig. VII-1) and is no guide to the position of the terminal part of the pterygoid.

The epitympanic wing bears a prominent sulcus for the ramus inferior (when that vessel is present; cf. figs. VII-1 and VII-2).

The epitympanic wing of the sphenoid is quite short in *Solenodon* and the piriform fenestra is correspondingly large (fig. VII-4). It is deeply grooved by the sulcus for the ramus inferior.

7.2.3 EPITYMPANIC WING OF THE SQUAMOSAL

An extremely large epitympanic wing of the squamosal is characteristic of tenrecs (figs. VII-1, VII-2). It is this outgrowth, rather than the tegmen tympani, which covers most of the ossicular chain and forms most of the epitympanic recess. In contrast to *E. europaeus* (6.2.3), the postglenoid foramen lies wholly within the squamosal.

In the sectioned specimens, the posterior part of the squamosal sends out a large descending wing which partly sheathes the proximal part of Reichert's cartilage (fig. VII-14). This projection is also found in adult tenrecs (fig. VII-2) and may be considered as the equivalent of the posttympanic process of other forms.

In *Solenodon* the epitympanic wing is relatively smaller than in tenrecs. However, it does complete the lateral half of the roof of the epitympanic recess (fig. VII-32).

In some of the large tenrecs and in *Solenodon* the area above the posttympanic process is modified into a broad, flaring plate (cf. *E. europaeus*, fig. VI-1). This flaring is absent in smaller genera, such as *Microgale* (fig. VII-3).

7.3 PRINCIPAL SPACES AND SEPTA OF THE MIDDLE EAR

As in Erinaceidae, there is no significant pneumatization of the middle ear in tenrecs or Solenodon. There is no hypotympanic sinus and the epitympanic recess is merely a shallow fossa in the posterior part of the epitympanic wing of the squamosal. The fossa incudis is well-developed, but there is no suggestion of a mastoid cavity in the fetus or adult.

Diverticulum D_3 is minute in all tenrecs and any rigorous attempt to separate it from the fossula fenestrae cochleae is pointless. In M. dobsoni, at least, the volume of D_3 appears to increase a bit through the moderate inflation of the CTPP in postnatal life. Nonetheless, the degee of difference between the late fetus and the adult is not very great.

The anterior part of the tympanic cavity, however, expands significantly in later ontogeny. This is mainly the result of continued growth at the basioccipital-basisphenoidal synchondrosis, which results in the lengthening of the entire basicranium. The epitympanic wings of the sphenoid and squamosal obviously keep pace with growth at the synchondrosis, for they fill most of the area in front of the anterior pole of the promontory.

MCDOWELL (1958:142) states that the CTPP of adult Solenodon "contains vacuoles apparently continuous with the mastoid cellulae". In the case of both the CTPP and mastoid area of MPIH 6863, these vacuoles or cellulae contain enlarged marrow spaces and are never air-filled (fig. VII-35). These spaces have no connexion with the epitympanic recess.

There are no septa of any significance in the available specimens.

7.4 MUSCLES, ARTERIES AND NERVES OF THE MIDDLE EAR

7.4.1 OSSICULAR MUSCLES

7.4.1.1 Tenrecidae

Both the tensor tympani and the stapedius are present in the sectioned specimens. The tensor tympani originates (in the young tenrec) from the membrane covering the piriform fenestra, the epitympanic wing of the sphenoid, and the epitympanic wing of the petrosal. Its fibers converge into a single tendon just in front of the level of the fenestra vestibuli; the muscle inserts into the malleus as usual. The otic ganglion supplies the tensor tympani (figs. VII-13, VII-22, VII-23, VII-29).

The stapedius arises from the side-wall of the auditory capsule and passes forwards in the capacious fossa formed by the posterior continuation of the crista parotica and the lateral side of the CTPP (figs. VII-8, VII-17, VII-25, VII-30). Its tendon passes through the fibrous tissue filling the foramen stylomastoideum medial to the VII nerve and inserts on the stapes (fig. VII-15). The muscle is supplied by the VII nerve, as usual.

The element of Paaw is absent in _H_. _semispinosus_, _S_. _setosus_, _M_. _dobsoni_ (this study) and _T_. _ecaudatus_ (FINDLAY 1944).

7.4.1.2 Solenodon

Solenodon does not differ significantly from Tenrecidae in regard to the origin and insertion of the ossicular muscles (figs. VII-32, VII-36).

7.4.2 ARTERIES

7.4.2.1 Introduction

The structural diversity of the auditory region in Tenrecidae is further underlined by significant variation in the cephalic arterial pattern. According to BUGGE (1974:30), the pattern in some tenrecids (e.g., Echinops telfairi) is very primitive, while in others (e.g., Tenrec ecaudatus) the pattern is the most advanced found among insectivores.

In terms of the vessels of interest here, arterial variation includes the fact that the ramus inferior is present in E. telfairi (BUGGE 1974), S. setosus (this study; see also ROUX 1947), M. dobsoni (this study) and probably all Potamogalidae (cf. GUTH, HEIM de BALSAC and LAMOTTE 1959), while it is completely absent in T. ecaudatus and H. semispinosus (this study; see also BUGGE 1974). It is likely that the ramus inferior is present in most other Tenrecidae as well (cf. MCDOWELL 1958), although this supposition is based on the presence of a foramen in the epitympanic wing of the sphenoid, not actual dissection. As noted earlier (7.1.7.1), this foramen sometimes transmits only the lesser petrosal nerve.

In species where the ramus inferior is absent, the mandibular and infraorbital arteries are fet by an anastomotic link with the internal carotid, the 'internal' maxillary artery. In cases where the ramus is present, the two anterior arteries receive their entire supply from this vessel (BUGGE 1974:104, fig. 4A).

There is also a prominent ramus posterior in all sectioned specimens. This vessel does not appear to have been previously described for tenrecs. Unlike the equivalent artery in *E. europaeus*, the ramus posterior of tenrecs shows no sign of involution in late fetuses.

Solenodon also possesses both the ramus inferior and the ramus posterior, although the latter artery has a somewhat different distribution than in tenrecs.

Vessel routes are illustrated in figs. VII-1, VII-2 and VII-4.

7.4.2.2 Stem and Major Tympanic Branches of the Internal Carotid Artery in H. semispinosus

The internal carotid is large and enters the tympanic cavity directly behind the posterior margin of the tympanic process of the basisphenoid (in older specimens in which the process is well-developed). Its foramen of entry is never well-circumscribed at any stage of development, and it is positioned beneath the middle of the medial side of the promontory rather than immediately in front of the ventral rim of the apertura fossulae fenestrae cochleae (cf. *E. europaeus*, fig. VI-1).

The artery does not actually cross the promontory, for it immediately divides after penetrating the fibrous membrane of the tympanic cavity (figs. VII-7a,b). Of the two branches arising from this bifurcation (the promontorial and proximal stapedial arteries), the stapedial was always the larger in the sectioned specimens.

From its origin, the promontorial artery strikes across the ventral surface of the promontory in a shallow sulcus (fig. VII-13) which leads it to the anterior carotid foramen (foramen caroticum primitivum in younger specimens) in front of the anterior pole of the promontory (fig. VII-12). The promontorial artery does not release a branch to the pterygoid canal.

The proximal stapedial follows a long, backward-curving course on the underside of the promontory, situated within a deep sulcus (fig. VII-14). The walls of its sulcus are confluent with the lateral section of the CTPP (figs. VII-15, VII-16, VII-17).

Immediately before entering the obturator foramen of the stapes (fig. 7a), the proximal stapedial gives off the ramus posterior (fig. 7b). At its origin, the latter vessel is by no means small; in the sectioned specimens, its diameter varied between one-half and two-thirds that of the parent vessel.

After leaving the proximal stapedial, the ramus posterior travels out of the tympanic cavity beneath the belly of the stapedius muscle. Instead of terminating within the stapedius fossa (as in E. europaeus fetuses), the vessel crosses the eminence formed by the posterior continuation of the crista parotica (figs. VII-8a,b,c) and rapidly ascends the posterolateral face of the pars canalicularis (fig. VII-18a). It finally breaks up into its terminal branches near the lambdoid suture and apparently feeds the muscles of the rear of the cranium. The ramus posterior does not form anastomoses (or at least any large ones) with other arteries.

From the obturator foramen of the stapes the proximal stapedial arches over the sulcus for the facial nerve (fig. VII-15) and (as the ramus superior) escapes into the cranial cavity through a large aperture (actually the posterior part of the piriform fenestra; see 7.2.1.1) lateral to the foramen faciale and medial to the tegmen tympani (fig. VII-14). The ramus inferior was not represented by so much as a twig in any of the sectioned specimens. If it is present at all during the ontogeny of H. semispinosus, it must obliterate very early.

7.4.2.3 Stem and Major Branches of the Internal Carotid Artery in S. setosus and M. dobsoni

Setifer and Microgale differ from Hemicentetes in possessing an unreduced ramus inferior. The course of the other tympanic branches of internal carotid (including the ramus posterior) is identical in all three. A vidian branch of the promontorial artery is not represented in either of the sectioned specimens of S. setosus (MPIH 1964/93) and M. dobsoni (MPIH 1964/103).

The ramus inferior is slightly larger than the ramus superior in S. setosus MPIH 1964/93, while in M. dobsoni MPIH 1964/103 they were equal in size. The ramus inferior is released by the proximal stapedial beneath the foramen for the ramus superior (figs. VII-23, VII-24) and follows a straight course across the roof of the tympanic cavity to the tympanic process of the alisphenoid (figs. VII-19, VII-20, VII-21, VII-22).

The internal carotid/promontorial and vertebral/basilar systems contribute equally to the supply of the brain in all tenrecs (cf. BUGGE 1974:131, table 1).

7.4.2.4 Sulci and Foramina

There is no sulcus for the internal carotid since that vessel does not really possess an intratympanic section (see 7.4.2.2). The sulcus for the proximal stapedial was consistently the deepest in both sectioned and macerated specimens, while that of the promontorial artery was the shallowest.

The sulcus for the ramus inferior is deeply etched into the epitympanic wing of the sphenoid in M. dobsoni and S. setosus adults. However, it should be noted that the sulcus contains veins and the lesser petrosal nerve as well as the ramus inferior (cf. E. europaeus 7.4.2).

The posterior carotid foramen does not approach the shape of a rounded aperture in any tenrecine, although the size of the membranous aperture given over to that vessel tends to be smaller in those species in which the tympanic process of the basisphenoid lies close to the CTPP (fig. VII-3).

A somewhat different condition obtains in Potamogalinae. The CTPP and tympanic process of the basisphenoid define between them a narrow aperture which is probably little larger than the diameter of the internal carotid itself (fig. VII-3).

The foramen for the ramus superior is produced by the closure of the posterior part of the piriform fenestra, as already noted (7.2.1.1). In the adult tenrec the foramen lies lateral or slightly anterolateral to the foramen faciale and is bounded by the epitympanic wing of the sphenoid anteriorly and the tegmen tympani and adjacent part of pars cochlearis posteriorly.

The foramen of exit for the ramus superior and lesser petrosal nerve (or the latter alone) has already been described in connexion with the tympanic process of the alisphenoid. It is usually complete in the adult, although in Potamogalinae it is confluent with the tympanic aperture of the auditory tube (fig. VII-3). It is still open ventrally in the sectioned specimens (e.g., fig. VII-20), but is obviously later closed over by the continued growth of the tympanic process of the alisphenoid.

The ramus posterior passes through the foramen stylomastoideum in all known cases, and thus does not possess its own aperture. There is a shallow sulcus originating in the foramen stylomastoideum which grooves the ventral aspect of the prominence of the ventral semicircular canal in adult *H. semispinosus* (fig. VII-2); this sulcus may contain the ramus posterior during life, although this is not certain. An equivalent sulcus could not be identified with certainty in the macerated skulls of the other species.

In *Potamogale velox* there is either an incisure or a complete foramen lying directly posterior to the stapedius fossa and foramen stylomastoideum. This feature is illustrated by both MCDOWELL (1958) (cf. fig. VII-3) and GUTH, HEIM de BALSAC and LAMOTTE (1959:442, fig. 19) but is not described or identified. It is possible that it accommodates the ramus posterior, although that vessel has not yet been identified in otter shrews. An equivalent foramen is either lacking in Micropotamogale or is incorporated into the rim of the foramen stylomastoideum (cf. GUTH, HEIM de BALSAC, and LAMOTTE 1959:442, fig. 18).

The anterior carotid foramen lies entirely within, or notches the posterior margin of, the epitympanic wing of the sphenoid. As pointed out by VAN KAMPEN (1905:424), the foramen pierces basisphenoidal material (i.e., the basisphenoidal part of the epitympanic wing). Interestingly enough, the basisphenoid surrounds the promontorial artery at its point of exit from the tympanic cavity by sending out small bony processes which envelop the degenerating alicochlear and anterior basicapsular commissures (conditions in H. semispinosus; see fig. VII-12). This development must be analogous to the production of the lingulae sphenoidales in Homo (DE BEER 1937:370).

7.4.2.5 Stem and Major Tympanic Branches of the Internal Carotid in Solenodon sp.

MCDOWELL (1958) provides an excellent description of the course of the internal carotid and its tympanic branches (including the ramus posterior) as they appear in the adult. Accordingly, only a brief description of conditions in the juvenile specimen of Solenodon sp. is needed here.

The internal carotid is large and enters the tympanic cavity just in front of the anteromedial side of the CTPP. It divides on the floor of the promontory into the proximal stapedial and promontorial arteries. An item not reported by MCDOWELL for the adult solenodon is that the diameter of the promontorial artery is not more than one-half that of the proximal stapedial.

The promontorial artery follows a normal course over the ventral surface of the promontory, then passes through the medial part of the piriform fenestra into the cranial cavity. It is not enclosed in a separate anterior carotid foramen.

MCDOWELL (1958:140), who was forced to work with specimens which had the arteries dried in place, states that the promontorial artery releases a vidian branch before entering the cranial cavity. However, the artery of the pterygoid canal is bilaterally absent in MPIH 6863. Only small veins accompany the deep and greater petrosal nerves into the pterygoid canal of this specimen.

The proximal stapedial has three branches, as in tenrecs: the ramus posterior, the ramus inferior, and the ramus superior.

Although MCDOWELL (1958:141, fig. 7B) depicts the ramus posterior as considerably smaller than the ramus superior or ramus inferior, in the sectioned juvenile the vessel (at its origin) is their equal in respect of luminal diameter (fig. VII-35). Further, MCDOWELL (1958:140) believed that the ramus posterior was distributed to foramina in the region of the foramen stylomastoideum. This is not the case, as the following description shows.

After arising from the proximal stapedial, the ramus posterior passes backwards, deeply grooving the anterolateral margin of the CTPP (fig. VII-35). Posterior to this point it is morphologically within the foramen stylomastoideum and is in close relation with the stapedius muscle and the VII nerve. The ramus posterior divides into two major branches within the foramen stylomastoideum. One branch travels posteriorly for a short distance before breaking up into a series of fine twigs beneath the belly of the stapedius muscle. Most of the twigs terminate within the stapedius fossa, although one curves back into the facial sulcus. On the whole, this branch appears comparable to the main body of the ramus posterior identified for tenrecs and at least young stages of _E_. _europaeus_, and is probably the one seen by MCDOWELL in adult solenodons.

The other branch passes anteriorly from the foramen stylomastoideum and arches around the tympano-styloid cartilage connecting the stylohyal to the tympanohyal (fig. VII-34a). It travels laterally from this position into the posterior part of the external ear, but it was not possible to trace the vessel to its final destination. The skin of the head and most of the external ear had to be removed before the specimen could be processed, for hair badly damages microtome blades. However, there are two likely possibilities regarding this anterior branch of the ramus posterior. First, it may constitute the principal artery of the external ear, having taken over part of the area of distribution of the posterior auricular artery of the external carotid. Alternatively, the anterior branch may represent an anastomotic link between the stapedial system and the true posterior auricular similar to the one alleged to exist in certain bats (DU BOULAY and VERITY 1973:27).

7.4.3 NERVES

The major nerves traversing the middle ears of tenrecs and Solenodon follow routes similar to those of the standard pattern (see fig. I-4).

(1) Facial (VII) Nerve

In the adult tenrec, the foramen faciale is located immediately in front of the anterodorsal margin of the foramen faciale. It travels backwards in a shallow sulcus in close relation with the ramus posterior of the stapedial artery and the tendon of the stapedius, and emerges from the tympanic cavity directly behind the tympanohyal.

In most adults the tympanohyal and the lateral section of the CTPP are in contact (or nearly so), and thus form between them a rudimentary foramen stylomastoideum definitivum (cf. E. europaeus, 6.4.3). This foramen is particularly well-circumscribed in Potamogalinae (fig. VII-3).

Solenodon does not depart from this general pattern except that in the adult the tympanohyal and CTPP do not appear to articulate (MCDOWELL 1958:140, fig. 6B).

(2) Chorda Tympani

The chorda tympani is released well beneath the foramen stylomastoideum. It passes laterally over Reichert's cartilage in the fetal tenrec and enters the tympanic cavity by passing above the posterior crus of the ectotympanic. There is apparently no canaliculus chordae tympani in the adult, and the chorda must therefore enter through the edge of the flaccid portion of the tympanic membrane.

The chorda, once in the tympanic cavity, follows a typical course; it travels over the medial face of the malleus, penetrates the gonial, and leaves the cavity by crossing over the sulcus malleolaris of the ectotympanic.

FINDLAY (1944:94, fig. 3b) found a small element of Spence adjacent to the manubrium of the malleus in a 47.4 mm CRL fetus of S. (=Ericulus) setosus. A cartilaginous process, now fused to the malleus, was found in this position in the slightly-older specimen of S. setosus (52.0 mm CRL) studied by me (fig. VII-24). However, it should be mentioned that in the latter specimen this process is not in close proximity to the chorda tympani.

An equivalent process could not be securely identified in the sectioned specimens of H. semispinosus or M. dobsoni. FLEISCHER (1973:143) identifies a blunt process on the occipital (posterior) face of the manubrium for adult "Ericulus telfairi" (probably Echinops telfairi), but does not relate it to the chorda tympani.

The chorda tympani of Solenodon follows a route similar to that of tenrecs. A foramen in the gonial for this nerve is present, but the element of Spence is not. As in certain tenrecs (fig. VII-3), the chorda tympani grooves the tympanic face of the entoglenoid process after leaving the sulcus malleolaris of the entotympanic (fig. VII-4).

(3) Internal Carotid Nerve and Deep Petrosal

The route of the internal carotid nerve is quite similar in tenrecs and Solenodon. The nerve arises from the cranial cervical ganglion, ascends the internal carotid and enters the tympanic cavity in company with that artery. The nerve bifurcates into medial and lateral branches immediately before or immediately after entering the tympanic cavity.

The nerve continues forwards in company with the promontorial artery to the anterior pole of the promontory. The lateral branch (now as the deep petrosal) comes into close relation with the greater petrosal, as the latter issues into the tympanic cavity through the piriform fenestra. The medial branch follows the promontorial artery into the cranial cavity (e.g., fig. VII-22).

The internal carotid nerve exchanges filaments with the small tympanic nerve at several points along its path.

(4) Greater Petrosal

This nerve is large, as usual. It arises from the geniculate ganglion, passes forwards between the trigeminal ganglion and the epitympanic wing of the petrosal, and then enters the tympanic cavity through the piriform fenestra. Thereafter, it travels coaxially with the deep petrosal.

(5) Nerves of the Pterygoid Canal

In all sectioned specimens, the greater petrosal and deep petrosal nerves enter the epitympanic wing of the sphenoid directly in front of the anterior carotid foramen (or foramen caroticum primitivum), well posterior to the probable location of the pterygoid bone. Accordingly, the tympanic aperture of the pterygoid canal cannot be used to separate pterygoidal from sphenoidal material in the adult.

(6) Auricular Ramus of the Vagus

As usual, the ramus auricularis travels from its origin in the posterior lacerate foramen to the rear of the stapedius fossa. It passes forwards beneath the belly of the stapedius and reaches the VII nerve as it emerges from the foramen stylomastoideum in the specimens of *H. semispinosus* and *M. dobsoni*. *S. setosus* MPIH 1964/93 differs in that the nerve enters a small ganglion (figs. VII-25a,b,c) on the posterior side of the VII nerve. This ganglion is apparently absent in the other sectioned specimens, although the ramus auricularis is very large in all cases.

The ramus auricularis does not penetrate the CTPP in the sectioned specimens, and its route is thus entirely extratympanic. However, SABAN (1956-57:60) records that a mastoid canaliculus (presumably in the substance of the CTPP) may be found in adult *Tenrec* (=*Centetes*).

MCDOWELL (1958:142) is correct in identifying a passageway for the ramus auricularis which cuts through the CTPP in adult *Solenodon*, for the mastoid canaliculus is present in the sectioned juvenile. The nerve does not actually enter D_3, but instead passes through the CTPP completely and emerges in the stapedius fossa. It courses over the dorsal surface of the muscle (instead of ventral to it, as in tenrecs) and, as usual, meets the VII nerve in the foramen stylomastoideum (figs. VII-35, VII-36).

(7) Tympanic Nerve and Lesser Petrosal

The tympanic nerve shows significant variability in the sectioned specimens. In the proximal part of its route it was clearly separate from the auricular ramus of the vagus only in the youngest specimen of *H. semispinosus* (figs. VII-8a,b,c). In the other specimens of *H. semispinosus* (cf. figs. VII-17, VII-18a) and in the fetus of *S. setosus* (cf. figs. VII-25a,b,c), it seems to be united with the ramus auricularis until just before the latter joined the VII nerve. Finally, the nerve could not be recognized at all in *M. dobsoni* MPIH 1964/103 (fig. VII-30a,b,c,d).

In *H. semispinosus* MPIH 1964/84 the tympanic nerve travels in close association with the ramus auricularis from their origins within the posterior lacerate foramen to the belly of the stapedius muscle. Unlike *E. fuscipes* and *E. europaeus* the nerve does not enter D_3 at all. Instead, it passes into the tympanic cavity beneath the tendon of the stapedius muscle (fig. VII-7). From here its route is typical, i.e., it crosses the proximal stapedial (fig. VII-7a), ascends the roof of the tympanic cavity lateral to the fossa for the tensor tympani (fig. VII-6), and meets a large filament from the geniculate ganglion.

Continuing forwards as the lesser petrosal nerve, it travels through the fibers of the tensor veli palatini out of the tympanic cavity beneath the developing alisphenoid (fig. VII-5).

In the two older specimens, and in the fetus of S. setosus, the tympanic nerve cannot be separately recognized until the major part of the combined ramus auricularis/tympanic nerve merges with the VII nerve. Otherwise, its route is as in MPIH 1964/84. In S. setosus the lesser petrosal accompanies the ramus inferior of the stapedial through the tympanic process of the alisphenoid.

In M. dobsoni the lesser petrosal arises from the geniculate ganglion alone, since the tympanic nerve is apparently absent.

The tympanic nerve is quite separate from the ramus auricularis in Solenodon. In this case, the nerve does enter D_3, through a small canaliculus in the CTPP which lies under cover of the larger passageway for the ramus auricularis. From here it travels through D_3, forms a small plexus with the internal carotid nerve where the latter enters the tympanic cavity, and crosses the proximal stapedial to the rear of the fossa for the tensor tympani. Within the fossa it joins with filaments from the geniculate to form the lesser petrosal. The lesser petrosal follows the ramus inferior of the stapedial out of the tympanic cavity to the otic ganglion.

7.5 SUMMARY OF PRINCIPAL FINDINGS

(1) The fibrous membrane of the tympanic cavity forms a significant part of the ventral wall throughout ontogeny, particularly in Solenodon.

(2) The bony ventral wall is variable in its composition. The tympanic process of the basisphenoid is well marked in most tenrecs,

but it is absent or vestigial in *Solenodon*. The caudal tympanic process of the petrosal is present in all investigated soricomorphs, although it is large only in *Microgale* and *Solenodon*. The rostral tympanic process of the petrosal is probably absent except perhaps in *Microgale*. The tympanic wing of the alisphenoid and the entoglenoid process of the squamosal may combine to form a high rampart around the anterior end of the tympanic cavity, as in *Tenrec* and *Solenodon*. The entotympanics are absent.

(3) The ectotympanic is slightly broadened to the lateral in the adult. It weakly articulates with the tympanic process of the basisphenoid in cases where the latter is formed. In *Microgale* and *Solenodon*, the posterior crus of the ectotympanic is fused with, or at least firmly joined to, the caudal tympanic process of the petrosal.

(4) The ectotympanic-tympanic process of the basisphenoid relationship is as in erinaceids (see 6.5).

(5) The dorsal wall is mainly formed by well-developed epitympanic wings arising from both the sphenoid and the squamosal. The tegmen tympani is rudimentary and the epitympanic process of the petrosal is also small.

(6) The piriform fenestra is often widely open in the adult stage.

(7) No significant degree of pneumatization occurs, and excavation of the bony walls of the tympanic cavity is negligible.

(8) The origin of the stapedius muscle is extratympanic throughout life. A ramus posterior of the stapedial artery exists in both tenrecs and *Solendon*, although its distribution is not entirely the same. Nerve routes are typical.

CHAPTER EIGHT

ANALYSES AND CONCLUSIONS

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- 8.1.2 Ontogeny
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8.1 SUMMARY: THE VENTRAL WALL

8.1.1 VARIATION IN COMPOSITION

Table 8-1 summarizes the distribution of various components of the ventral wall among the forms studied here. The ectotympanic is not listed because it is a constant member. Notation merely reflects whether a particular component can be identified according to the definitions presented in appendix II, without regard to size.

This table only lists forms which I have been able to study by means of serially-sectioned and macerated specimens. Although variation within the orders can be easily determined by reference to the works cited in each chapter, some general statement about the composition of the ventral wall in the four groups will be useful in connexion with later discussions. Accordingly, within-group variation is briefly covered in the following paragraphs, with some attention to relative size of components and relevant fossil evidence.

Primates

> Ventral wall composed of the petrosal plate and ectotympanic, the latter being either phaneric or aphaneric.

As far as is known, the entotympanics are not represented in any living or fossil primates (SZALAY 1972b; see 8.5.5). The ectotympanic is never broadened medially to a significant degree, although it varies greatly in its lateral extent (SZALAY 1975). The entoglenoid process may spread onto the anterolateral extremity of the petrosal

Table 8-1

VARIATION IN THE VENTRAL WALL OF THE MIDDLE EAR

	RE	CE	RTPP	CTPP	EPS	TPB	TPA
PRIMATES							
Microcebus	A	A	P	P	A	A	A
Lemur	A	A	P	P	A	A	A
Propithecus	A	A	P	P	A	A	A
Galago	A	A	P	P	A	A	A
Loris	A	A	P	P	A	A	A
TUPAIOIDEA							
Tupaia	P	?A	A	P	A	A	A
MACROSCELIDEA							
Elephantulus	P	P	P	P	P	P	P
LIPOTYPHLA							
Erinaceus	A	A	P	P	?P	P	P
Hemicentetes	A	A	A	P	P	P	P
Setifer	A	A	A	P	P	P	P
Microgale	A	A	?P	P	P	P	P
Solenodon	A	A	A	P	P	?A	P

A, not present; P, present

RE, rostral entotympanic; CE, caudal entotympanic; RTPP, rostral tympanic process of petrosal; CTPP, caudal tympanic process of petrosal; EPS, entoglenoid process of squamosal; TPB, tympanic process of basisphenoid; TPA, tympanic process of alisphenoid plate, but it never actually faces on the middle ear cavity. The same applies to the broad flanges which arise from the basioccipital and external pterygoid plate and attach to the bulla in Tarsius. Tympanic processes of the alisphenoid and basisphenoid are wholly absent. Complete bullae are invariably present.

Tupaioidea

> Ventral wall composed of an entotympanic and a minute caudal tympanic process of the petrosal, except in Ptilocercus where a large tympanic process of the alisphenoid completes the anterior part of the bulla. Ectotympanic always aphaneric.

If Anagale (?Oligocene, As.) is not related to tree shrews (MCKENNA 1963), there is no evidence for the ancestral condition of the tupaioid ventral wall. Adapisoriculus of the European Paleocene is regarded as a tupaioid by VAN VALEN (1965) but its auditory region is unknown. The entotympanic of Tupaiinae appears to be a rostral entotympanic. The entoglenoid region of the squamosal never faces on the middle ear cavity. The tympanic process of the basisphenoid is probably absent, or is so reduced that its character cannot be determined in modern tree shrews. The tympanic process of the alisphenoid is absent or reduced to a low crest in Tupaiinae. The bulla is always complete.

Macroscelidea

> Ventral wall composed of the rostral and caudal entotympanics and tympanic processes of the petrosal, squamosal, basisphenoid, and alisphenoid. Ectotympanic always phaneric.

Although the dental evidence for this order extends back to the Oligocene of Africa (PATTERSON 1965; BUTLER 1969; BUTLER and HOPWOOD 1957), the auditory region of fossil macroscelideans is unknown.

VAN DER KLAAUW (1929) has shown that the composition of the ventral wall is much the same in all modern elephant shrews, although I disagree with him that the tympanic process of the basisphenoid is entirely absent. The bulla is always complete.

Lipotyphla

> Ventral wall usually, but not always, formed by a caudal tympanic process of the petrosal, tympanic processes of the basisphenoid and alisphenoid, and entoglenoid process of the squamosal. The ectotympanic is phaneric or semiphaneric.

The Recent lipotyphlans are more variable than members of the other three orders, although there are some underlying similarities in composition. The entotympanics are evidently absent in all families (but see 8.5.4). The caudal tympanic process of the petrosal is virtually absent in a few tenrecs (e.g., Tenrec), but tends to be fairly large in other families. The rostral tympanic process of the petrosal is noticeable only in Erinaceidae, although minute ridges occupying the correct position can be seen in certain soricids and tenrecs. The entoglenoid process of the squamosal is enlarged in tenrecs and Solenodon, but barely evident in Soricidae (despite the fact that it is modified to clasp the mandible in shrews as well). In at least some Erinaceidae, the entoglenoid region is flat and not built into an identifiable process. In species with complete bullae (some talpids and all chrysochlorids), the entoglenoid does not face on the middle ear cavity. Although a well-defined tympanic process of the basisphenoid is a lipotyphlan characteristic, it is not present in all Recent families. It is absent or vestigial in soricids and Solenodon. The tympanic process of the alisphenoid is minute in all cases, and is merely an extension of the line of the entoglenoid onto the alisphenoid (MCDOWELL's 1958 'preotic crest'). Fossils which can be assigned to modern lipotyphlan families with some confidence do not vary significantly from living members (see BUTLER 1948, 1956, 1969; MCDOWELL 1958; RICH and RICH 1971).

8.1.2 ONTOGENY

Tympanic processes of the mammals studied here nearly always arise as periosteal outgrowths from their parent bones; this is in agreement with findings in other mammals (STARCK 1975). The caudal tympanic process of the petrosal, however, initially arises in cartilage. During its cartilaginous stage the caudal tympanic process tends to be small, and most of its increase in size is accomplished after ossification. The entotympanics present special problems in interpretation and are separately discussed in section 8.5.

The ontogeny of tympanic processes is comparatively simple. They arise as trabeculae of young, woven bone and their growth is typically rapid. Remodelling often converts the woven bone to lamellar bone with few or no haversian systems. Components also display great regularity in their place of origin: they arise either adjacent to the fibrous membrane (tympanic processes) or within the membrane itself (entotympanics).

Functionally, the ventral wall (whether composed of membrane, cartilage or bone) serves to delimit an air-filled space (the middle ear) and to protect that cavity from deformation by underlying structures. Bony elements permit the middle ear cavity to increase in size during ontogeny in cases where they undergo a significant degree of pneumatization. Increase in volume is important, since it can reduce the stiffness reactance of middle ear impedance and thus increase auditory sensitivity (see 8.3).

The growth of chondro-osseous components in the ventral wall is probably conditioned in large measure by genetically determined potentials of basicranial bones. It is difficult to believe that they are induced (in the embryological sense) by the fibrous membrane, despite their close relationship with the latter. The fibrous membrane is not under tension prior to the formation of tympanic processes, since it is laid down well before the cavum tympani has expanded to a significant degree. However, the fibrous membrane may play some sort of role in controlling the growth of components after their initial differentiation.

Since muscles do not often arise from tympanic processes, it follows that the former play little part in the formation or shaping of such processes. The only constant exceptions to this include the tensor and levator veli palatini, which attach to components in the anterior part of the ventral wall. Both muscles are small and only occasionally cause the formation of muscular processes. The origins of other muscles, such as the digastric (posterior belly), rectus capitis lateralis and longus capitis, may occasionally transgress onto one or another of the tympanic processes. However, their shaping influences are invariably minor.

None of the tympanic processes investigated here show any sign of having had a previously independent existence. There is no evidence that any of them are suppressed entotympanics (see 8.5).

8.1.3 PRIMITIVE VS. DERIVED STATES

8.1.3.1 Introduction

It is clear from discussions in previous chapters that paleontologists have focused a great deal of attention on the composition of the ventral wall. Embryological studies can, of course, define composition for living taxa, but their bearing on evolutionary interpretations is otherwise indirect. On the other hand, because such studies can be carried out at levels of anatomical resolution normally unavailable to the paleontologist, they can provide new and potentially valuable approaches to character analysis. Assessments of character states and homologies generally improve with increasing knowledge regarding the nature and function of the structures of concern. Fossils will always provide the clearest guide to the course of evolution, but the recognition of relationships ultimately depends on the rigour with which character analysis and the separation of primitive, derived, and convergent states can be carried out.

In this section, an attempt is made to improve some of the existing character analyses of the ventral wall.

Determination of the primitive and derived states of any character requires a knowledge of what has gone before as well as what has come after (today's plesiomorphies are yesterday's apomorphies). The anatomy of living representatives (if any) of a group must first be accurately assessed. This neontological evidence may then be compared to existing fossil evidence relevant to the group in question. While this procedure will permit certain _prima facie_ deductions about primitive vs. derived states, it still remains to be seen whether or not any of these states are primitive for a much wider number of forms. Directionality in the change of form (or 'morphocline polarity') may then be deduced with fair confidence, and correlated changes in different taxa can form the basis of evolutionary hypotheses.

8.1.3.2 _Ancient Eutherian Morphotype_

Primates, tree shrews, macroscelideans and lipotyphlans are unlikely to have had a common ancestry which extended beyond the latest Cretaceous. Accordingly, conclusions regarding the derived features of their ventral walls relative to one another must, in part, be based on character states found in early eutherian mammals.

Unfortunately, the few truly early basicrania of eutherian mammals are too incomplete to shed much light on the problem of primitive conditions. As a result, rather more weight has to be placed on neontological evidence, with a corresponding diminution in the reliability of projections.

In any event, SZALAY (1975) has recently provided a provisional morphotype for the eutherian ventral wall. His conclusions, both written and pictorial, are that (1) a 'tympanic process of the petrosal' was present (partly equivalent to the caudal tympanic process of the petrosal of this study), (2) ancient eutherians may have had bony bullae, and (3) an entotympanic may have been present, but this remains to be proven.

SZALAY's first point is likely to be correct for two reasons. First, the caudal tympanic process of the petrosal is found on isolated eutherian petrosals of the latest Cretaceous, and also exists in Didelphodon, a large marsupial of equivalent age (MACINTYRE 1972). MACINTYRE also regards the caudal tympanic process as an ancient feature, although he adds that the great development of this process is a specialization away from the primitive (general therian) condition.

Secondly, this process is extremely widespread among modern mammals. In addition to my studies, which indicate that it is a constant (if not always significant) element of the ventral walls of primates, tree shrews, macroscelideans and lipotyphlans, other workers have identified it in mammals as diverse as the pholidotan Manis (STARCK 1941) and the chirpoteran Rousettus (VAN DER KLAAUW 1922). If my interpretations regarding the supposed 'entotympanic' of metatherians are correct (see 8.5.5), this process may also be present and well-developed in the majority of living marsupials.

Embryological evidence adds finer resolution to character analysis in this case. The caudal tympanic process schematically illustrated by SZALAY (1975:95, fig. 1) is restricted to a position directly behind the apertura fossulae fenestrae cochleae. In previous chapters it has been shown that in modern mammals the caudal tympanic process extends lateral to this position, either by continuing along the medial side of the stapedius fossa or by joining with the posterior continuation of the crista parotica. In the eutherian placentals of the Bug Creek Anthills quarry (figures by MACINTYRE 1972), the line of the caudal tympanic process extends along the medial side of the stapedius fossa in a way very reminiscent of the equivalent structure in modern *Erinaceus*. The ridge on the medial side of the stapedius fossa may still be present, even if other parts of the caudal tympanic process are reduced. This seems to be the case in the palaeoryctid *Didelphodus* (early-middle Eocene, N.A.).

Finally, it may also be noted that a caudal tympanic process of the petrosal was apparently absent in non-therian mammals of the Mesozoic. The prominent crest adjacent to the apertura fossulae fenestrae cochleae in the multituberculates *Kamptobaatar* and *Sloanbaatar* is identified as a paroccipital process by KIELAN-JAWOROWSKA (1970), and it probably is. However, this process might have done a double duty (i.e., served as an attachment for the depressors of the mandible as well as a posterior border for the middle ear).

SZALAY's features (2) and (3) are linked, because the first bullae may have been entotympanic in origin. In section 8.5 I review the case for the antiquity of the entotympanics. It is one of my conclusions that independent elements have long been associated with the eutherian ventral wall, but their homologies are problematical (i.e., the elements now grouped under the term 'entotympanics' may have appeared at different times in different lineages). It is true that evidence for complete bullae, however formed, is non-existent for Cretaceous eutherians (see MACINTYRE 1972). However, it remains possible that one or the other of the entotympanics might have been present, but fell away after death. For example, the entotympanic of the early Tertiary mammal Leptictis is rarely preserved, although there is sufficient evidence to indicate that it was definitely present (MCKENNA 1966). Nonetheless, even in Paleoene and Eocene mammals a complete bulla is rare (the primates being a prominent exception).

Should other tympanic processes be added to the morphotype? The rostral tympanic process of the petrosal is not nearly so common among living mammals as in the caudal tympanic process (see VAN DER KLAAUW 1931), although it is by no means limited to the primate-lipotyphlan group. A large one exists in elephant shrews, and it may well be present in a number of marsupials as well as other eutherians. The fossil evidence for its antiquity is meagre (again excepting primates). It is not represented on the petrosals of Bug Creek eutherians (MACINTYRE 1972). A bony excrescence is found on the ventral surface of the promontory in Microsyops and Leptictis, but SZALAY (1969) and others interpret this crest as a rugosity upon which the (?entotympanic) bulla rested (cf. conditions in modern Tupaia).

A low crest fronts the anterior part of the auditory region in most modern lipotyphlans. As we have noted, this crest is made up of the entoglenoid portion of the squamosal and a small tympanic process of the alisphenoid. In groups with complete bullae (e.g., lemurs), the same two processes may slightly overlap the anterior surface of the bulla. VAN DER KLAAUW (1931) notes that this ridge ('preotic crest' of MCDOWELL 1958) is relatively common in extinct and extant memmals (especially lipotyphlans sensu lato). Conditions in latest Cretaceous eutherians are unknown since only isolated petrosals are known, but the ridge is identifiable in Leptictis and Palaeoryctes. Whether a small tympanic process of the alisphenoid is a derived character state relative to the general therian morphotype is an open question (the process is large in many marsupials; see GREGORY 1910; VAN DER KLAAUW 1931; MCDOWELL 1958), but the evidence seems fairly positive that this crest is also an ancient eutherian feature.

The ectotympanic was presumably ring-like or only slightly expanded to the lateral in ancient eutherians, and thus did not provide a significant tympanic component. There is no evidence that the basisphenoid formed a tympanic process until the middle Tertiary (BUTLER 1948, 1956).

Combining the evidence discussed in previous pages, the following conclusions may be made about the eutherian morphotype for the ventral wall:

(1) the probably non-hypertrophied middle ear was bounded fore and aft by a low crest, formed respectively by the squamosal-alisphenoid and the petrosal;

(2) the rest of the ventral wall may have been completely membranous, or it may have carried an entotympanic;

(3) contributions by the basioccipital and basisphenoid were absent, and the ectotympanic was probably more or less ring-like.

8.1.4 DERIVED STATES OF THE PRIMATE VENTRAL WALL

SZALAY (1975) lists two character states of the ventral wall which he feels are primitive for primates (and possibly other eutherians related to primates to an unknown degree): (1) the petrosal bulla and (2) the 'shielding' of the apertura fossulae fenestrae cochleae by the canal for the internal carotid artery. Embryological evidence permits a closer analysis of how these features arise in modern primates and how they differ from conditions found in other mammals.

The petrosal bulla is a composite structure in the limited sense that it arises from caudal and rostral tympanic processes. Although these processes fuse into a single rampart (the petrosal plate) early in bullar ontogeny, they follow slightly different patterns of development and do not invariably occur together in other mammals. Accordingly, they should be separately evaluated whenever possible.

I suggest that the caudal tympanic process of primates differs from the eutherian morphotype in that it traverses the whole of the mastoid region and encloses the origin of the stapedius muscle. It differs in the same way from the caudal tympanic processes of tupaioids and erinaceomorphs, the groups to which primates are most often compared. Whether this character state is unique to primates among all mammals remains to be proven, however. For example, ROUX's (1947) illustrations of the developing auditory region of *Eremitalpa* indicate that the stapedius may be wholly sealed within the middle ear in chrysochlorids.

There do not appear to be any singular features of the primate rostral tympanic process, except for the large size it attains in certain families. The macroscelidean rostral tympanic process is probably as large, relatively speaking, as that of hominoids. However, no other mammals approach the degree of elaboration found in strepsirhines and *Tarsius*.

The 'shield' described by SZALAY (1975) has a peculiar ontogeny in modern lemurs. As explained in section 2.3.2.3, pneumatic activity excavates the rear of the petrosal plate in such a way that a bony lamella is left adjacent to the apertura fossulae fenestrae cochleae. This lamella (posterior septum of this study) is separated from the true bullar wall in the adult by a small diverticulum, and occupies the same position as the medial part of the original caudal tympanic process of the petrosal. The available ontogenetic evidence indicates that the 'shield' is a derivative of the latter process, and not a new formation *per se*.

Small crests partly or wholly envelop the internal carotid as it enters the tympanic cavity in macroscelideans and some erinaceomorphs. However, in these forms pneumatic activity does not deeply penetrate the substance of the petrosal plate, and no shield is formed. The shield is missing or barely indicated in lorises, no doubt because the method of petrosal pneumatization is radically different from the lemuriform pattern. SZALAY (1975) records that the shield is found in Phenacolemur among the Plesiadapiformes.

In summary, the derived characters of the primate ventral wall (relative to the eutherian morphotype) include:

(1) a caudal tympanic process of the petrosal which surrounds the origin of the stapedius muscle, sealing it within the middle ear cavity;

(2) a very large rostral tympanic process of the petrosal which arises from the length of the promontory and which extends entirely around the anterior part of the middle ear cavity;

(3) a 'shield' (posterior septum), produced by the pneumatization of the rear of the petrosal plate, which obscures the apertura fossulae fenestrae cochleae.

Character state (1) appears to be characteristic of all modern primates and extinct Tertiary primates "of modern aspect" (SIMONS 1972; see SABAN 1963 for detailed descriptions of the stapedius muscle in Recent forms). However, I am not convinced that it is characteristic of Plesiadapiformes. Although the bulla of the specimen of Phenacolemur illustrated by SZALAY (1972a) is badly broken, my mental reconstruction of the disposition of the petrosal plate leaves the stapedius fossa outside the middle ear cavity.

Pneumatization strongly affects the size of the rostral part of the petrosal plate, and it is also responsible for the appearance of the shield-like posterior septum in my view. Plesiadapiformes and Lemuriformes probably share character states (2) and (3) because of a similar pattern of pneumatization in both cases.

The problem of whether or not entotympanics ever existed in the primate line is separately considered in section 8.5.5.

8.1.5 RELATIONSHIPS OF THE ECTOTYMPANIC

8.1.5.1 Introduction

The relationships of the ectotympanic to components of the ventral wall tend to be fairly constant within major groupings of mammals at the family level or higher, judging from VAN DER KLAAUW's (1931) descriptions. These relationships, stated as taxonomic characters, have assumed an important place in the higher-category taxonomy of a few groups, such as primates, tree shrews and carnivores. Nonetheless, the tendency towards constancy should not be overemphasized or treated uncritically when assigning weights to characters (MACPHEE 1977).

In preceding chapters, ontogenetic factors controlling the development of relationships were identified and partially evaluated on a taxon-by-taxon basis. In this section, major findings are brought together with a view towards establishing a simple, general explanation of how different relationships arise and undergo modification.

The comparative embryological approach to the explanation of form is to search for correlations and regularities in development and then to suggest cause-effect linkages. Such non-experimental analyses cannot directly demonstrate that a given set of factors is responsible for a given set of ontogenetic events, nor reveal at what morphogenetic levels these factors interact. Despite these inherent weaknesses, I believe that this approach permits the extraction of valuable first approximations which may be tested by other, more refined techniques as appropriate. The explanations of form offered here should be taken as such approximations.

In this discussion, the term 'relationship' will stand for 'the topographical relationship of the ectotympanic to a component of the ventral wall'.

8.1.5.2 Some Factors

The final (adult) condition of any relationship is achieved through the interplay of various factors or shaping influences. The ones which I have been able to isolate may be grouped under the headings of growth, pneumatization and soft-tissue influences. These will first be discussed in relation to tympanic processes of basicranial bones; the entotympanics present a few special problems and will be evaluated separately.

The difference between growth and pneumatization is an arbitrary one, but it is helpful to make a distinction here. I base my contrasting use of these terms on the rate and location of bone-building or bone-remodelling activities. Thus 'growth', as used here, means the slow, essentially ventrad elongation of a tympanic process produced by the formation of new bone on its free margin. 'Pneumatization', on the other hand, refers to the unusually rapid formation and destruction of opposing surfaces of a component.

Soft-tissue influences resolve into the effects of the fibrous membrane and sutural tissues. Tympanic processes do not arise in random locations. The comparative data fully establish that such processes always arise adjacent to the surfaces of the fibrous membrane, then grow to varying degrees along the membrane towards the ectotympanic. As I have stated elsewhere, this correlation implies to me that the fibrous membrane serves as a bed or substrate which directs the growth of components along a given plane.

Sutural tissues bind bone edges together, among other things. Their degree of elaboration can affect the final condition of a relationship, for in cases where they are deficient or absent the continued action of other factors may result in the covering of the ectotympanic by a tympanic process to a greater or lesser degree.

8.1.5.3 Derivation of Relationships

Fig. VIII-1 is an attempt to illustrate diagrammatically how different factors can produce different relationships, depending on their relative importance or influence. The outcomes portrayed in this figure are probably not exhaustive, although most relationships known to me are depicted.

Topographically, every relationship begins as an athictic one, since components are necessarily small before they are large. It is legitimate to suppose that tympanic processes have increased in size during mammalian evolution as a result of improvements in middle ear efficiency. Broadly speaking, the athictic condition is probably primitive or early in both the ontogenetic and the phylogenetic sense. However, this does not mean that one can call every athictic relationship primitive, as secondary reduction of tympanic processes

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undoubtedly occurs. This is suggested by the tympanic process of the alisphenoid of tree shrews (large in the supposedly more primitive Ptilocercus, vestigial or absent in Tupaiinae) and perhaps the RTPP of erinaceids (large in Miocene hedgehogs, relatively small in modern ones).

The athictic condition in the adult stage is structurally and ontogenetically the simplest outcome, in that no significant relationship exists between the ectotympanic and the component in question. Essentially, nothing happens to the process beyond its initial induction and growth.

Other conditions can be considered as derivatives of primordially athictic relationships. These outcomes depend on the action of the other factors described above. If growth continues but sutural tissues do not form or form incompletely, then the degree of pneumatization will affect the final condition (right side of fig. VIII-1). If, on the other hand, sutural tissues are fully elaborated, bone territories will remain in contact throughout ontogeny even if pneumatization is extensive (left side of figure VIII-1).

Several sub-categories or types of relationships can be characterized by reference to the position and development of the ectotympanic. At least three types or outcomes result from incomplete sutural tissue development. A small or insignificant degree of pneumatic activity within the tympanic cavity results in the semiphaneric condition of the ectotympanic (fig. VIII-1c); normally, the latter bone does not form an elongated bony external acoustic meatus (e.g., tenrecs, hedgehogs). Extensive pneumatization combined with non-expansion of the anulus produces the unique aphaneric condition of tree shrews and lemurs (fig. VIII-1d). However, a third arrangement should probably be included here, although its exact ontogenetic basis is unknown. In certain polyprotodont marsupials, rodents and subfossil Malagasy lemurs, the hypotympanic sinus extends far beneath the part of the ectotympanic which holds the tympanic membrane (fig. VIII-1e). The ectotympanic displays lateral broadening in these cases, and its external margin may extend beyond the bullar wall (thus both aphaneric and semiphaneric conditions may result). In the case of the marsupials and the lemurs (see WOOD JONES and LAMBERT 1939 and SZALAY 1975), the ontogeny of this condition may feature the initial overgrowth of the anulus by the expanding tympanic process (alisphenoid or petrosal plate), followed by a later lateral broadening of the ectotympanic. I assume that this condition is the result of imperfect development of sutural tissues and extensive pneumatization (cf. modern lemurs and the aphaneric condition), although no data exist on this matter. The situation in rodents expressing this condition (e.g., Gerbillinae; LAY 1972) is somewhat different, as the entire bulla is ectotympanic in origin. Sutural tissues play no role, and the subtympanic extension of the hypotympanic sinus beneath the crista tympanica is completely determined by the effects of pneumatization. Since the ectotympanic is fully exposed in rodents no matter what the style of pneumatization, the condition is properly a phaneric one.

In my sample, fully phaneric conditions of the ectotympanic are always associated with a complete elaboration of sutural tissues. I believe that the reason for this is that sutural tissues must be present in order to keep bone territories in tandem. It appears to be a fairly easy matter for a growing tympanic process to delaminate the fibrous membrane from the ectotympanic in cases where sutural tissues are absent, and so to produce semiphaneric or phaneric outcomes. However, further studies may reveal that phaneric conditions can be produced in the absence of sutural tissues, and so I have enclosed this outcome in brackets on the right side of fig. VIII-1.

The outcomes depicted in figs. VIII-1f and VIII-18 differ only in whether or not the ectotympanic fuses with the adjacent tympanic process. Both are conditioned by sutural tissues, for the comparative evidence shows that a phaneric outcome will result no matter how extensively the bulla is pneumatized. Further, fusion is not correlated with the degree of intratympanic pneumatization (cf. tympanic process of alisphenoid in macroscelideans vs. petrosal plate in lorises).

8.1.5.4 Ectotympanic-Entotympanic Relationships

Since entotympanics form within the fibrous membrane (see 8.5), it is surprising to me that they do not invariably cover the ectotympanic in cases where they grow to large size. However, the only documented example of such overgrowth is the relationship found in tree shrews. In all other situations, sutural tissues are apparently formed and overgrowth prevented (e.g, macroscelideans).

At present, I can only suggest that the aphaneric condition is reached because the fibrous membrane is not attached to the ectotympanic (cf. section 4.1.6). In effect, there is nothing to keep the ectotympanic and entotympanic in tandem since sutural tissues are not formed, and the entotympanic can freely grow around the anulus. Although the lack of a definite connexion between the fibrous membrane and the ectotympanic in young tree shrews is definitely unusual, it cannot be the whole explanation. The fibrous membrane, after all, is easily delaminated from the ectotympanic and such delaminations occur in other cases.

8.1.5.5 Evolution of Relationships in Primates

I have pointed out in chapters 2 and 3 that ectotympanic relationships have assumed a particularly important place in primate taxonomy. Indeed, some concepts of primate evolution rely very heavily on presumed sequences of modification in these relationships (e.g., GINGERICH 1973; SZALAY 1975).

The utility of these sequences, in my view, is reduced by the rather simple nature of the development of ectotympanic relationships in modern primates (and, by projection, in ancestral primates as well). Nearly all of the relationships depicted in fig. VIII-1 have appeared at one time or another in primate evolution (see SZALAY 1975:118, fig. 16), and this variability indicates to me that they are no sure guide to the geometry of phylogeny (MACPHEE 1977).

Further, it must be admitted that characters based on relationships are not as clear-cut as many students think. A few examples will bring this point out clearly. In some adult lorises the bone of the petrosal plate around the styloid fossa may be built outwards to a small extent, and so cover a part of the posterior crus of the ectotympanic (SABAN 1963; CARTMILL 1975). In lorises, _Tarsius_ and probably some anthropoids, lamellar bone is laid down over the external side of the original suture between the ectotympanic and petrosal plate. In South American primates with narrow ectotympanics (e.g., _Ateles_), the petrosal plate may slightly cover the lower margin of the ectotympanic (SABAN 1963). Conversely, in Old World anthropoids the ectotympanic grows _medially_ to a limited extent, thus covering a part of the petrosal plate (SABAN 1963; ANSON, BAST and RICHANY 1955). All of these examples may be regarded as intermediates between the supposed extremes of the classic phaneric dichotomy. I do not mean to imply that broad types of relationships cannot be discriminated at all, for they can. However, the purpose of character analysis is not served by ignoring apparent exceptions.

8.2 SUMMARY: THE DORSAL WALL

8.2.1 VARIATION IN COMPOSITION

Complete accounts of the composition of the dorsal wall are rarely provided in the literature on the mammalian auditory region. While this wall is not as variable as the ventral, there are significant differences in the four orders in regard to the relative size of components and the degree of their exposure (table 8-2).

Within-group variation (as far as it is known) is briefly considered below.

Table 8-2

VARIATION IN THE DORSAL WALL OF THE MIDDLE EAR

	TT	EWP	EWSq	EWSp
PRIMATES	+++	+++/+	++	(+)
TUPAIOIDEA	+++	(+)	+	(++)
MACROSCELIDEA	+++	++	--	+++
LIPOTYPHLA	+/++	+	+++/+	+++/+

+ = small size

++ = medium size

+++ = large size

/ = or

( ) = indicates wing in question is hidden by other components

-- = absent

TT = tegmen tympani

EWP = epitympanic wing of petrosal

EWSq = epitympanic wing of squamosal

EWSp = epitympanic wing of sphenoid

Primates

> Dorsal wall composed of outgrowths of the petrosal with a small contribution by the epitympanic wing of the squamosal.

A large tegmen tympani is characteristic of primates (DE BEER 1937; SPATZ 1964; STARCK 1962). The substantial pneumatization of the petrosal plate from within the tympanic cavity proper creates a very large epitympanic wing of the petrosal. In lorises this wing is minute, due to the differing method of pneumatization. Its incidence in other primates is unknown, but it is probably small.

The epitympanic wing of the squamosal is not especially large, although it forms part of the roof of the epitympanic recess. The epitympanic wing of the sphenoid is mostly alisphenoidal in origin. It is usually covered by the tegmen tympani and epitympanic wing of the petrosal, as in lemurs, although in lorises and perhaps *Tarsius* (see figures in SABAN 1963) a small part of it is exposed. In higher primates the sphenoid is not found in the dorsal wall (VAN DER KLAAUW 1931).

All that remains of the piriform fenestra is a narrow fissure between the epitympanic wing of the petrosal and the tegmen tympani, which in many cases can be obliterated.

Tupaioidea

> Dorsal wall of complex form. The moderately well-developed epitympanic wing of the sphenoid is partly or almost entirely covered by a dorsal extension of the entotympanic. The tegmen tympani is well-developed, but the epitympanic wing of the squamosal is narrow.

Tupaioids appear to be unique among mammals in the degree to which the entotympanic extends dorsally onto the roof of the middle ear. When this part of the entotympanic is stripped away (fig. IV-4), a configuration is left which does not depart too greatly from that found in lipotyphlans (particularly erinaceomorphs). The dorsal part of the entotympanic is less extensive in Ptilocercus than in Tupaiinae.

The tegmen tympani is not inferior in size to that of primates. A wide fissure (the true piriform fenestra) separates the epitympanic wing of the sphenoid from the dorsal outgrowths of the petrosal, but it is covered by the entotympanic in the adult (fig. IV-4).

Macroscelidea

> Dorsal wall closed by wings of the petrosal and sphenoid. The epitympanic wing of the squamosal is entirely lacking.

The tegmen tympani is of a size equivalent to that of tupaioids. The lack of an epitympanic wing of the squamosal is interesting, but it is probably not unique to elephant shrews (see VAN DER KLAAUW 1931). A considerably broadened anterior crus of the ectotympanic is fastened to the lateral edge of the tegmen tympani, occupying the place where one would expect to find the epitympanic wing of the squamosal.

The remnant of the piriform fenestra is represented by the petrosphenoid suture.

Lipotyphla

> Dorsal wall usually bears a pronounced epitympanic wing of the sphenoid. Tegmen tympani and the epitympanic wing of the petrosal always small and often minute. Epitympanic wing of squamosal small except in tenrecoids.

The dorsal wall, like the ventral wall, is quite variable in lipotyphlans compared to conditions in the other three orders.

The tegmen tympani and the epitympanic wing of the petrosal usually play no important role in bounding the dorsal wall. It should be noted that in erinaceids the petrosal contribution to the dorsal wall appears to be rather large because of the hollowing out of the mastoid eminence.

The wings in the anterior part of the roof do not always grow to a significant extent, which accounts for the enormous piriform fenestra of some species. Thus in soricoids none of the components of the dorsal wall grow very much during ontogeny, leaving a wide aperture in the adult skull. In tenrecs growth is more extensive, although the piriform fenestra is still fairly wide in the adults of most species. In most erinaceomorphs growth is sufficient to reduce the fenestra to a narrow fissure (the petrosphenoid suture).

It is unlikely that the anterior part of the roof in talpids is formed by the basisphenoid alone, as PARKER (1886) and VAN KAMPEN (1905) state. As in other insectivores, some contribution must be made by the alisphenoid (see also 1.4.2).

The extremely large epitympanic wing of the squamosal found in tenrecs is apparently also characteristic of chrysochlorids, judging from VAN KAMPEN's (1905) notes. The frontal and orbitosphenoid are exposed in the epitympanic recess of golden moles according to SIMONETTA (1957a), due to the tremendous degree of pneumatization of this part of the dorsal wall.

Published descriptions of the dorsal walls of extinct members of the persistent lipotyphlan families indicates that there has been little change in composition during the Tertiary (see BUTLER 1948, 1956, 1969; MCDOWELL 1958; RICH and RICH 1971).

8.2.2 ONTOGENY

There is nothing remarkable about the development of epitympanic wings. The wings of the squamosal and sphenoid grow periosteally, while the tegmen tympani and often the epitympanic wing of the petrosal first appear as cartilaginous outgrowths of the auditory capsule.

The major extrinsic factors influencing their growth are the expanding neural mass and the growth of the basioccipital-basisphenoidal synchondrosis. Both factors promote the widening of the piriform fenestra; the epitympanic wings usually compensate for this widening by growing towards each other until the fenestra is closed over.

Pneumatization also affects the conformation of the dorsal wall at specific sites (see 8.3).

8.2.3 PRIMITIVE VS. DERIVED STATES

The eutherian morphotype for the dorsal wall has not yet been explored by paleontologists. However, it probably differed little from that found in modern erinaceomorphs (piriform fenestra reduced to a narrow fissure, broad contact between the epitympanic wing of the sphenoid and dorsal outgrowths of the auditory capsule, and a rather small epitympanic wing of the squamosal.

A widely open piriform fenestra is restricted to a few, invariably small, mammals. VAN VALEN (1966) believes that it has appeared independently in several lineages, and is no indicator of phyletic relationships. All that embryology shows is that the fenestra is a persistently unossified part of the cranial wall (see GASC 1963). MOFFETT (1972) has suggested that cleft palate may result from the failure of the palatal suture to form. Although this example is teratological, it underlines the importance of sutural growth to cranial morphogenesis, whether or not one considers sutures to be sites of secondary, compensatory growth (MOSS 1960, 1971). A process can be envisaged whereby epitympanic wings will begin to form according to the genetic potentials of their parent bones, but will fail to cover the piriform fenestra completely if sutural tissues are not elaborated at a critical ontogenetic stage

SIMONETTA (1957b, 1963) feels that the fenestrae of Myosorex and Talpa, together with other anatomical features of their skulls, may play a dubious role in cranial kinesis. However, he nonetheless considers kinetic mechanisms in mammalian skulls to be highly specialized features.

Broad areas of close contact between the sphenoid and petrosal are an inheritance from Mesozoic mammals. While large apertures are found in the contact areas of these forms, they have been interpreted as foramina for divisions of the mandibular nerve (KERMACK and KIELAN-JAWOROWSKA 1971).

The squamosal is normally an insignificant bone in non-therians. Its introduction into the roof of the tympanic cavity is undoubtedly a late development in mammalian evolution.

8.2.4 DERIVED STATES OF THE PRIMATE DORSAL WALL

As previously noted, primates are distinguished from the other mammals included in this survey by the degree to which the petrosal contributes to the dorsal wall.

It is difficult to make out sutures in the dorsal walls of early Tertiary plesiadapiforms, but the petrosal appears to have made about the same contribution found in modern lemurs (see illustrations in RUSSEL 1964; SZALAY 1972a, 1975). During the course of primate evolution the tympanic wing of the sphenoid was more or less covered over by petrosal outgrowths (although it can still be made out in serial sections). An analogous situation occurs in tree shrews, but it is the entotympanic, not the petrosal, which covers the epitympanic wing of the sphenoid in tupaioids.

The epitympanic wing of the squamosal is only slightly enlarged relative to the projected eutherian morphotype. Participation of the squamosal in the roof of the epitympanic recess is very common in modern eutherian mammals (VAN DER KLAAUW 1931).

8.3 SUMMARY: PRINCIPAL SPACES AND SEPTA

8.3.1 PNEUMATIZATION AND MIDDLE EAR ANATOMY

I have shown in some detail in preceding chapters that pneumatization has profound effects on the form of the middle ear during ontogeny. The most obvious effect of pneumatization is the grossly swollen auditory bullae characteristic of numerous small mammals. However, there can be other effects as well: the style of pneumatization may condition the relationship of the ectotympanic to components of the bony ventral wall, and the placement of foramina. Indeed, the consequences of pneumatic activity are far-reaching, and its influence on form should always be taken into account during character analysis.

It is simple enough to observe that the middle ear increases in volume during development through the growth and remodelling of the bony surfaces which face on it. Such processes are not random, but affect different parts of the presumptive middle ear in varying and species-specific ways. One of the difficulties in speaking about the ontogeny of the principal spaces is that anatomical language does not adequately bring out the _Gestalt_ of total middle ear development. Yet it is the total pattern which is the most important from both the taxonomic and functional points of view. Dividing the middle ear into a series of named spaces has a certain value, but it should be remembered that these are terms of convenience which may obscure more than they reveal. I have tried to show that _how_ spaces develop makes a great deal of difference to the naming procedure. Thus the strict positional division of principal spaces in lorises and lemurs, as advocated by SABAN (1963) clouds the fact that the lorisiform 'hypotympanic sinus' does not develop at all like that of lemurs, and should be called by a different name.

On the other hand, there is a limit beyond which neither ontogeny nor position will permit a decision regarding proper homologies. Thus pneumatic activity originating within the tympanic cavity proper strongly affects the ventral walls of lemurs, tree shrews and elephant shrews, leading to a voluminous space which is much the same in all three cases. This space must be called a hypotympanic sinus in all three instances on the basis of its development and position, but it would be foolish to pretend that this space, by itself, has any taxonomic value.

It may be a more successful approach to let positional names take a secondary place to the pattern of development of principal spaces. This can be done by describing from whence a space initially develops and how it expands in size. I have attempted to illustrate how this can be done for strepsirhines (see 8.6.1), a group in which pneumatization has important effects on a number of highly-weighted basicranial characters.

8.3.2 INFLUENCE OF MIDDLE EAR CAVITIES ON ACOUSTIC PERCEPTION

The data collected in this study are of no particular value to the analysis of middle ear function. At the same time, it is hardly unreasonable to assume that some of the more important structural differences described here have some relation to the acoustic requirements and adaptations of the mammals concerned. The extremely detailed studies of OAKS (1967), LAY (1972) and WEBSTER and WEBSTER (1975) on various families of rodents reveal that important deductions can be made about acoustic perception on the basis of middle ear morphology.

One subject which is beginning to attract the attention of physiologists interested in mammalian acoustic perception is the form and function of the auditory bulla and the principal spaces of the middle ear (TONNDORF and KHANNA 1968; DALLOS 1973). In a general way, it is possible to conclude from theoretical considerations that a relatively large middle ear should enhance sensitivity in the lower range of the audible sound spectrum (see appendix I). The correlation is simple: stiffness is more important than mass in impeding acoustical energy at lower frequencies. Since stiffness is contributed in part by the air contained within the middle ear, an enlarged middle ear cavity will have reduced stiffness and it will take correspondingly less sound pressure to activate the tympano-ossicular system. Conversely, large middle ears should not appreciably affect higher-frequency sensitivity (i.e., frequencies above the resonant frequency), since high-frequency sensitivity is conditioned by mass. This conclusion is borne out by the experiments of WEBSTER and STROTHER (1972) on heteromyid rodents.

However, when one turns to actual cases the correlation is far more complicated, since other factors exert an influence. The shapes of the principal spaces affect reactance (MØLLER 1972), as do other components of stiffness (see appendix I). WEBSTER and WEBSTER (1975) have shown that certain heteromyids are extremely sensitive to low frequencies not only because the middle ear cavities are enormous, but also because numerous reductions in the stiffness supplied by the tympanic membrane, ossicular ligaments, tendons of the ossicular muscles and anular ligament have also occurred. Accordingly, one cannot simply assume that a mammal with a relatively large middle ear is also very sensitive to low frequencies. This consideration should be remembered when making evaluations of the auditory sensitivity of fossil mammals.

It may be pointed out that, while *Lemur*, *Galago* and *Tupaia* may be considered to have large middle ears, and while their low-frequency sensitivity is better than that of *Didelphis* and *Hemiechinus*, they are all exceeded to a significant degree by anthropoids, *Canis*, *Felis*, *Procyon*, and many other mammals (see data of MASTERTON *et al*. 1969; GILLETTE *et al*. 1972). There are no data for macroscelideans, but I suspect that they do not possess conspicuous low-frequency sensitivity either.

8.4 SUMMARY: MUSCLES, ARTERIES AND NERVES

8.4.1 OSSICULAR MUSCLES

The tensor tympani normally arises from one or more structures: the fore part of the petrosal, the rear of the sphenoid, and the tubal canal. WERNER (1960b) suggests that an origin which is mainly located on the sphenoid (as in *Ornithorhynchus*) is primitive, since the tensor tympani is probably a derivative of the internal pterygoid muscle of non-mammals.

The common site of origin for most of the fibers of the tensor tympani in the mammals studied here is the area directly lateral to the anterior pole of the promontory. In Macroscelidea and Lipotyphla the muscle extends onto the epitympanic wing of the sphenoid as well. In strepsirhines and other primates its origin lies entirely on the petrosal (and the tubal canal, which is formed by the petrosal).

The origin of the stapedius muscle always lies within part of the broad depression in the mastoid region which is encircled by the gyrus of the lateral semicircular canal. In primates (and perhaps chrysochlorids) the origin of the stapedius lies entirely within the middle ear because of the method of development of the caudal tympanic process of the petrosal. In most erinaceids, tenrecids, soricids and Solenodon the stapedius fossa is completely exposed or only very slightly covered by the lateral section of the caudal tympanic process. Tupaioids, macroscelideans and talpids with complete bullae are intermediate in the sense that the origin of the muscle is still visible on the side wall of the skull, but the stapedius fossa is reduced to a narrow canal or fissure.

That the stapedius muscle is not fully incorporated into the middle ear cavity in many cases causes no surprise, since it is really a levator hyoidei (GOODRICH 1930) which originates in second-arch material and which inserts on another second-arch derivative--the stapes. It is said to arise in the same blasteme as the digastric (posterior belly) and stylohyoideus (WERNER 1960b), and may represent all that is left of the depressor mandibulae.

The only other finding which requires some further discussion is the absence of the tensor tympani in the specimens of Tupaia glis (see 4.4.1). Complete absence of this muscle is extremely rare, and its loss or marked reduction has previously been regarded as an adaptation for low-frequency acuity on the part of certain fossorial mammals (e.g., the talpid _Scalopus_; see HENSON 1961). Despite their name, tree shrews vary greatly in the degree of their arboreality (MARTIN 1968a). However, by no stretch of the imagination can they be regarded as fossorial mammals. Furthermore, the data of HEFFNER, RAVIZZA and MASTERTON (1969) and MASTERTON, HEFFNER and RAVIZZA (1969) reveal that _T. glis_ displays no unusual degree of low-frequency sensitivity. Its audiogram shows a somewhat better sensitivity in the lower frequency range than the hedgehog _Hemiechinus auritus_, for example, but several of the other mammals utilized in these studies exceed the tree shrew by significant margins (e.g., man, racoon, cat).

Even if SABAN (1963) is correct in asserting that the tensor tympani is present in (other) tree shrews, the muscle he illustrates is very small, as is the stapedius muscle. Thus the absence of pronounced low-frequency acuity is all the more surprising, since both the reduced size of the ossicular muscles and the relatively voluminous middle ear cavity of tupaioids suggest diminished stiffness reactance (see WEBSTER and WEBSTER 1975).

8.4.2 ARTERIES

The major purpose in presenting sections on the tympanic branchings of the carotid was to demonstrate that microanatomical techniques can bring out important details concerning arterial patternings which are easily missed with other methods. Some examples include the identification of a persistent ramus inferior of the stapedial artery in Tupaia and a ramus posterior in all investigated lipotyphlans, and the demonstration that the intrapetrous section of the artery of the pterygoid canal is absent in several of the forms in which it was thought to be present.

On the other hand, it was not supposed that this study would contribute a great deal of new information concerning the carotid system. There is no point in presenting a review on the mammalian carotid system here, as I can add little to the discussions of BUGGE (1974), SZALAY (1975) and others. However, the taxonomic significance of certain arterial patterns is briefly discussed under the headings of section 8.6.

8.4.3 NERVES

No attempt was made to describe the fine structure or complete distribution of the nerves traversing the middle ear. If only routes and chief connexions are considered, the general picture is one of insignificant variation among the mammals described here.

Nonetheless, reconstruction of the routes of nerves in fossil and macerated skulls is often of some anatomical interest. Difficulties in reconstruction include the facts that the nerves of the middle ear are not usually encases in canals or deep sulci, and that they often share foramina with blood vessels. The following points may be helpful to other students:

(1) Whenever it is possible to identify the posterior carotid foramen, it is safe to conclude that the internal carotid nerve enters

that foramen if no other aperture is present in the immediate vicinity. The internal carotid artery and nerve are invariably closely associated.

(2) Whenever it is possible to identify a foramen of exit for the ramus inferior of the stapedial artery, it is safe to conclude that the lesser petrosal nerve passes through the same aperture if no other is present. However, a very small aperture in the tympanic process of the alisphenoid indicates that only the nerve is present and that the ramus inferior is obliterated (case in certain tenrecs).

(3) Bony apertures for the tympanic nerve and auricular ramus of the vagus, if they exist at all, will always lie behind the point of entry of the internal carotid artery and nerve, in more or less close proximity to the posterior lacerate foramen. This disposition of foramina is important, as the tympanic nerve is sometimes confused with the internal carotid nerve in anatomical descriptions.

(4) The posterior aperture of the pterygoid canal may lie on the lip of the anterior carotid foramen or slightly in front of the latter. Mere presence of the pterygoid canal is not evidence for the existence of a vidian artery, as the canal often holds only the deep and greater petrosal nerves and a small vein.

(5) The routes of the facial nerve and chorda tympani are usually fairly simple to determine, since there is a wealth of comparative data on these nerves. The foramen faciale was difficult to identify in the macerated skulls of some tenrecs, as it opened adjacent to the foramen for the ramus superior. The chorda tympani

does not always possess a bony canaliculus, as it may perforate the pars flaccida of the tympanic membrane or the fibrous tissue between the posterior crus of the ectotympanic and the squamosal.

Since the topography of these nerves is seemingly much the same in all mammals, their routes may have some limited use as reference points against which differences in bony structure may be compared. For example, it is apparent from observation that the strepsirhine CTPP initially bounds a diverticulum D_3 which is much larger than in the other forms investigated here. This finding is also suggested by the fact that the route of the auricular ramus of the vagus is entirely intratympanic in these prosimians, but extratympanic in the others. Later in ontogeny there can be some convergence toward the primate condition in cases where the bone of the CTPP grows around part of the ramus (e.g., Solenodon). However, the path of the nerve remains extratympanic, properly speaking. LAY (1972) uses the path of the auricular ramus to show how the petromastoid is differentially pneumatized in species of gerbilline rodents.

Two matters of gross anatomy deserve further attention than can be given here. First, the small to minute size of the tympanic nerve in all the mammals investigated in this study was an unexpected finding, inasmuch as the same nerve is relatively large in Homo. This may indicate that its distribution is less complex than in man, a finding which is supported by the small size of the tympanic plexus.

Secondly, although I have followed HIGBEE's (1975) argument to its logical conclusion by naming 'nerves of the pterygoid canal' (see appendix II), it must be admitted that the greater and deep petrosal nerves appear to blend into a single nerve as they enter the pterygoid canal in the forms investigated here. The only mammal other than *Homo* in which the deep and greater petrosal nerves are known to be separate along their entire routes is *Pan* (STARCK 1960). Accordingly, until anatomical matters are further clarified, the usage of 'nerves of the pterygoid canal' should be taken to mean that the fibers of the parent nerves may remain entirely independent although they travel coaxially and in one sheath.

8.5 ENTOTYMPANICS, EMBRYOLOGY AND EVOLUTION

8.5.1 INTRODUCTION

Histological origin is not the same as phylogenetic origin, as GAUPP (1900), DE BEER (1937) and many others have pointed out. Yet a consideration of the embryogeny of structures can be of great value to our understanding of their possible courses of evolution. For example, skeletal elements usually arise in the same positions and from the same primordia in broadly-related forms, despite evident differences in architecture, size and relations in adult stages. This constancy of embryonic patterns of development is primary evidence of homology, and has permitted several brilliant morphological insights (such as the identities of the auditory ossicles in higher vertebrates) which could not have been so readily achieved through the analysis of adult structure alone.

However, instances of non-concordance in developmental patterns do exist, and in these situations it is a difficult matter to know what value should be assigned to embryological data. The entotympanics fall into this category, and our knowledge of their homologies and evolutionary history is quite unsatisfactory.

Most embryological interpretations of the entotympanics may be fitted within one of two schools of thought, which hold respectively that:

(1) the entotympanics are detached portions of other structures, and have thus acquired their developmental independence through subdivision;

(2) the entotympanics are *sui generis*, and do not owe their origin to the subdivision of other elements.

In addition, a wider set of studies relating to the adult basicranial anatomy of extinct and extant mammals have added a third proposition, that:

(3) entotympanics, in several cases, have undergone suppression and now arise as outgrowths of other elements.

I will note here that, perhaps as a direct result of uncertainty about which of (1) and (2) is more likely to be correct, speculation under (3) has been carried to unwarranted limits.

The evidence pertinent to the ontogenetic origins of the entotympanics in modern mammals will be presented and evaluated first.

This will be followed by a review of relevant fossil evidence and a reconsideration of the incidence of the entotympanics in Recent forms. Finally, the evidence for suppression and associated topics will be discussed, with particular attention given to the origins of the tympanic processes of the petrosal and the identities of the bullae of tupaioids and primates.

8.5.2 THE EVIDENCE OF EMBRYOLOGY

There are only a handful of published observations on the ontogeny of the entotympanics. Of these, some are useless in the present context because an insufficient number of specimens were studied, or because macerated materials alone were used.

Rostral Entotympanic

The rostral entotympanic displays two different forms of initial development, according to adequately detailed studies. Its primordium arises separately in *Rousettus*, *Galeopithecus*, macroscelideans (VAN DER KLAAUW 1922, 1929), and *Myotis* (FRICK 1954); but in *Procavia* (VAN DER KLAAUW 1922), *Dasypus* (REINBACH 1952), and *Tupaia* (SPATZ 1966) it is continuous with the cartilage of the auditory tube from the start.

The evidence of primordial relations is thus evenly split between independent vs. dependent development of the rostral entotympanic. Arguing from this to possible evolutionary sequences, two routes are equally likely without further analysis. The first possibility is that the tubal cartilage alone existed in ancestral mammals, but in several lineages it has subdivided into a tubal cartilage proper and a rostral entotympanic (the latter presently showing varying degrees of independence from its parent element). The second possibility is that, anciently, the rostral entotympanic arose as a structure distinct from the tubal cartilage, but now exhibits varying degrees of fusion with the latter.

Since the available data are incompatible, it is not possible to make more than an informed guess as to which possibility is the more likely. However, my own feeling is that the later fate of the primordium of the rostral entotympanic supports the notion that it is a derivative of the tubal cartilage.

In *Rousettus*, *Galeopithecus* and probably most if not all macroscelideans, the primordium of the rostral entotympanic rapidly coalesces with the posterior parts of the tubal cartilage. This brings conditions in these forms more into line with what has been observed in *Procavia*, *Dasypus* and *Tupaia*. Furthermore, even in the cases of separate chondrification, the chondral centers for the tubal cartilage and rostral entotympanic are embedded within a continuous field of mesenchyme or procartilage. Many cartilages of the skull, which could not have arisen through the fusion of separate elements during evolution, arise from more than one center of chondrification (DE BEER 1937).

Also, there are other instances of old structures being put to a novel use in mammals. Examples include the ala temporalis and the tegmen tympani, which arise from the pterygoquadrate cartilage (dorsal cartilage of the first branchial arch) and crista parotica respectively. The latter two structures are extremely ancient features of the vertebrate cranium, but in therian mammals they have acquired a new function--they help form part of the 'new' side wall of the neurocranium (DE BEER 1937). The cavum epiptericum is an entirely extracranial space in higher vertebrates other than mammals, but in therian mammals it becomes included within the skull through the hyperdevelopment of the lamina ascendens of the ala temporalis and its associated ossification, the alisphenoid. The tegmen tympani, also a mammalian creation, serves a similar function farther back on the skull, for the primitive condition was to have the posterior side wall end flush with the suprafacial commissure (which covers the facial nerve as it enters the cavum supracochleare).

Indeed, the growth of the entotympanics and the ala temporalis-alisphenoid is analogous in more than one respect, for both expand within dense connective tissue membranes (fibrous membrane of the tympanic cavity and membrana spheno-obturatoria of the side wall; see below and see GOODRICH 1930:268).

It must still be recognized that there are serious impediments to a simple derivation of the rostral entotympanic from the cartilage of the tube. For example, there is a pronounced tendency for cartilaginous rudiments to fuse into a solid mass during ontogeny. Many of these are devoid of phylogenetic significance, and have been developed to stabilize the various elements making up the chondrocranium (DE BEER 1937; STARCK 1962).

There are other, more specific, problems as well. If the anterior mass of cartilage described for youthful stages of _Tupaia_ (see 4.1.3) comprises a single unit, why does a strip of cartilage around the auditory tube remain into adult life while the rest of the mass ossifies endochondrally? Why is a definite perichondrium/periosteum eventually formed between this strip of cartilage (which is presumably the equivalent of the tubal cartilage of other mammals) and the rostral entotympanic, if they constitute a single unit. Observations like these would normally imply secondary fusion and therewith the essential independence of the tubal cartilage and the entotympanic.

It is obvious that the available data are simply insufficient for a final resolution of the problem of the ontogenetic origin of the rostral entotympanic. For this reason, I see no point in doing away with the term 'rostral entotympanic' and replacing it with some other, such as 'tubotympanic' (= cartilage of the auditory tube + rostral entotympanic; REINBACH 1952). The use of REINBACH's term involves a prior decision about the derivative nature of the entotympanic which we are really in no position to make.

Caudal Entotympanic

Although the number of well-documented studies is no greater, it is possible to be somewhat more conclusive about the ontogenetic origins of the caudal entotympanic.

On the basis of a very limited set of observations on young stages of *Pteropus* and *Dasypus*, VAN KAMPEN (1915) proposed that the entotympanic (by which he meant the caudal entotympanic, the only one known to him) is a derivative of the second branchial arch.

Although he claimed that the caudal entotympanic was primordially continuous with Reichert's cartilage in these forms, almost every study other than his has found that this association occurs very late in ontogeny, when it occurs at all. None of VAN DER KLAAUW's (1922) specimens, which included examples of Pteropus and Dasypus, displayed the kind of inseparable continuity between the caudal entotympanic and Reichert's cartilage that is generally characteristic of the relations of the rostral entotympanic and the tubal cartilage. In addition to the above, there is no primordial fusion in Rousettus, Galeopithecus, Canis, Procavia (VAN DER KLAAUW 1922), Myotis (FRICK 1954), Bradypus (SCHNEIDER 1955) or macroscelideans (VAN DER KLAAUW 1929), although the last two cases are not strictly comparable since the caudal entotympanics of the three-toed sloth and elephant shrews are intramembranous ossifications.

The only author who has supported VAN KAMPEN's derivation is REINBACH (1952), again on the basis of conditions in the nine-banded armadillo (Dasypus).

On the whole, then, it seems likely that the caudal entotympanic of most mammals possessing this element is properly an independent development of the ventral wall which does not owe its origin to the material of the second branchial arch. This is important, for in most cases 'the' entotympanic of fossil mammals is probably a caudal entotympanic. In those Recent mammals for which good data exist, the rostral entotympanic is usually much smaller than the caudal entotympanic. The few exceptions include hyraxes, the 'type A' carnivores of HUNT (1974) and Tupaia (in which the rostral entotympanic forms the entire bulla except for a minute contribution by the CTPP).

Histological Diversity, the Fibrous Membrane, and the Origin of the Entotympanics

Embryologists have chiefly been concerned with whether or not the entotympanics can be derived from the tubal cartilage and Reichert's cartilage. However, there are two other aspects of entotympanic development which have never been properly evaluated. In my view, they have an important bearing on our understanding of the nature and origins of these enigmatic elements.

The first aspect concerns the difficulty of classifying entotympanics within the traditional classes of endochondral bones and intramembranous bones. As already noted, there is great uniformity in the ontogenetic origins of most elements of the skeleton. Thus the ectotympanic and the bones of the vault always arise in membrane, while most of the bones of the basicranium show the familiar two-stage form of endochondral ontogeny in which ossification centers appear in a cartilaginous matrix.

Yet in the case of the entotympanics, if all reports are to be believed, diversity reigns. The histological characteristics of their primordia in different species have been variously compared to hyalin cartilage, young elastic cartilage, 'secondary' cartilage, chondroid tissue, metaplastic osseous tissue, and intramembranous bone. While some of these assertions are probably wrong, it is unquestionable that at least two styles of origin occur. In the majority of cases the entotympanics develop from cartilage (although they do not always ossify). But in Bradypus and, in my view, Elephantulus, the caudal entotympanic develops like an intramembranous bone.

This diversity in histological origin may be of no consequence. It may be that entotympanics which now arise in membrane are truly homologous with those that arise in cartilage, through the suppression of the cartilaginous matrix or acceleration of the time of appearance of the ossification center. Certainly, there are instances of membrane-bones having become cartilage bones during evolution, and vice versa (DE BEER 1937). However, most of these cases are restricted to fish, and such reversals are almost unknown in mammals.

The second aspect concerns the relationship of the fibrous membrane to formed elements of the ventral wall, including the entotympanics. In my studies, I found that entotympanics differ from all other such components in that the former differentiate or primarily grow within the fibrous membrane, while the latter differentiate outside the membrane but grow along it.

Heretofore this relationship has not been considered especially significant, and it is difficult to know whether the intimate association of the entotympanics and the fibrous membrane noted above always occurs. However, a review of the relevant literature indicates that the association is definitely common.

VAN KAMPEN (1905:328, 448) was the first to note the presence of the fibrous membrane in an animal with an entotympanic. In a neonatus of Tupaia he was unable to find entotympanic cartilage, but he did note that the 'bulla' at this stage consisted of a thin sheet of connective tissue extending between the auditory capsule and the ectotympanic. This thin sheet is definitely the fibrous membrane; sixty years later, SPATZ (1966:399) completed VAN KAMPEN's note by observing that the posterior spur of the entotympanic is enclosed within it.

On the basis of fetal conditions in the vespertilionid bat, Miniopterus, FAWCETT (1919) argued that both the cartilage of the tube and the entotympanic arise in the same strand of connective tissue which surrounds the first branchial pouch. This strand of connective tissue is evidently the fibrous membrane, for the tympanic cavity is a derivative of the first branchial pouch. Significantly, a well-developed fibrous membrane is also known in another vespertilionid, Myotis; FRICK (1954:70-71, 75, 97) drew particular attention to the fact that in this bat both entotympanics appear within a homogeneous sheet of connective tissue situated beneath the auditory capsule.

It is not clear from his descriptions or illustrations how often the entotympanic elements were associated with a fibrous membrane in the series of young specimens studied by VAN DER KLAAUW in 1922. However, he specifically mentions (1922:152) for Dasypus that the caudal entotympanic is situated within a sheet of connective tissue which must, by its position and relations, be the fibrous membrane. REINBACH (1952:6), in his study of the same form, confirms this association.

Fortunately, VAN DER KLAAUW (1929:526) was very clear in his later paper on bullar ontogeny in elephant shrews:

> In all specimens we find in the 'ventral' wall of the tympanic cavity a thin membranous plate formed by an accumulation of the cells of the connective tissue which is in this plate more dense. In the oldest specimens this plate of more dense connective tissue forms the periosteum and perichondrium of the rostral petrosal plate, and of the rostral and caudal entotympanic.

Of particular interest is his description of the histogenesis of the caudal entotympanic (1929:534):

> ...cells of the more dense connective tissue alter into cartilage cells which in turn alter into bone cells; perhaps a number of them omit the stage of the cartilage cell. The material seems to indicate that the 'Zellenknorpel' may be an ontogenetic stage in the development of bone. No doubt the histogenesis of the caudal entotympanic is worth a special investigation, as we may expect that the development of this skeletal element, which develops not in very young embryos, but at about birth in already differentiated connective tissue and which very soon ossifies without passing a hyalin cartilaginous stage, will show features quite different from ossification in cartilage as it is generally known.

The only other modern author who has actually postulated that the fibrous membrane gives rise to elements in the ventral wall is REINBACH (1952:33-35). However, he did not restrict himself to the entotympanics. Instead, he maintained that the tympanic process of the basioccipital (of the porpoise, Phocaena) and the tympanic process of the basisphenoid (of Chrysochloris, Setifer and other insectivores) appear to develop within the fibrous membrane also. His general conclusion was that this membrane has skeletogenic potential; elements formed by it can be produced either in bone or in cartilage, and may ossify independently or from the basioccipital or basisphenoid.

I attach the following significance to the set of observations outlined in previous pages. First, the diversity of histological origins which have been reported may be prima facie evidence that the entotympanics (especially caudal entotympanics) of different mammals may not be truly homologous. That is, the elements generally classified under the term 'entotympanics' may have arisen not once, but several times. This view would at least make some sense of the fact that entotympanics are found in some, but not all, members of what are normally considered to be fairly logical taxonomic and phyletic groupings (see VAN DER KLAAUW 1931).

Secondly, I conclude that the markedly different style of association between the fibrous membrane and the entotympanics, compared to other components of the ventral wall, is further evidence that the entotympanics are not simply disconnected parts of other elements. The only exception to this that I would make is the rostral entotympanic, which may be a derivative of the tubal cartilage.

However, there are some other matters which require further clarification. It was mentioned that REINBACH (1952) claimed that the fibrous membrane had skeletogenic potential. I reject this claim for tympanic processes, which are always surrounded by periosteal tissues derived from their parent bones. However, inasmuch as the entotympanics differentiate, or at all events, grow within the fibrous membrane, one may ask whether this membrane directly gives rise to them.

The appearance of skeletal elements within already differentiated dense connective tissues is not at all uncommon. WEIDENREICH (1930) provides an extensive catalogue of heterotopic ossifications (penis bones, 'heart' bones, tracheal bones, etc.) which, although not universal in distribution, tend to be rather constant within certain groups. Neither periosteum nor endosteum in the traditional sense exist in the locations where many of these elements appear. At most, the dense connective tissues can be said to have a 'periosteal quality', i.e., they are capable of forming chondro-osseous structures.

If a real difference exists between 'true' bones and heterotopic bones, it turns on whether or not the pre-existing matrix is calcified or ossified in the absence of identifiable osteoblasts (HAINES and MOHUIDDIN 1968). In the case of the rostral entotympanic of Tupaia, the cartilaginous matrix appears to be much like that of other endochondral bones. This is not the case with the anlage of the caudal entotympanic of Elephantulus. While I believe that the method of growth of the caudal entotympanic of the latter form bears a closer resemblance to that of membrane-bones than cartilage-bones, the cells around which matrix is elaborated may be mesenchymal cells interspersed within the fibrous membrane, and not osteoblasts per se. It is beyond the powers of non-experimental studies to give an answer to this question.

In summary, the following points have the backing of the majority of embryological observations on the origins of the entotympanics:

(1) the rostral entotympanic may represent an extension of the tubal cartilage, which has acquired a certain degree of developmental independence and a center of ossification in some species;

(2) the caudal entotympanic is a unique ossification of the ventral wall of the middle ear which does not owe its origin to second-arch material;

(3) the entotympanics of different mammalian groups may have arisen at different times. This appears to be especially true of the caudal entotympanic, and may explain why its anlagen vary in different species.

The very late fusions of the entotympanics with other bones are no more significant to the resolution of the problems of interest here than is the fusion of the bones of the vault in adult higher primates. However, such fusions are common (VAN DER KLAAUW 1930, 1931), and represent one source of difficulty in recognizing the existence of entotympanics in adult stages.

8.5.3 THE EVIDENCE OF FOSSILS

I do not intend to review in detail the incidence of entotympanics in fossil mammals, since I have not seen original specimens. Moreover, none of the fossil evidence is Mesozoic in age and therefore has little bearing on the origins problem. Numerous examples and descriptions of entotympanics in fossil mammals are provided in VAN DER KLAAUW's (1931) monograph. HUNT's (1974) study, which attempts to characterize primitive and derived states of the entotympanics in carnivores, is the only detailed report of its sort in the recent literature.

The only groups known to possess the entotympanics are all mammalian. For this reason, VAN KAMPEN (1905) claimed that the entotympanic(s) were mammalian neomorphs, on the footing that no homologues for them could be found in lower vertebrates. This interpretation has been followed by all later authors (e.g., VAN DER KLAAUW 1922, 1931; STADTMÜLLER 1936; REINBACH 1952; STARCK 1967). However, consensus on this issue might be regarded as inevitable, since no one other than VAN KAMPEN has made a systematic study of this aspect of the homology problem. Table 8-3 presents an overview of the homologies which have been suggested during the last century or so.

While VAN KAMPEN's (1905) mammalian innovation theory remains unchallenged, it is important to be clear about the quality of its substantiating data. To be blunt, there is no evidence, other than negative or indirect evidence, which touches upon the phylogenetic origins of the entotympanics. We cannot identify with any degree of precision the group in which they first appeared, or when. While it appears certain that one or the other of the entotympanics existed in several eutherian lineages by the late Paleocene-early Eocene, the time of their origin must have been much earlier, barring the possibility of multiple inventions. Elucidation of this matter must await further relevant fossil discoveries.

Since the course of mammalian evolution was not well understood at the time of VAN KAMPEN's researches, he could not be specific about

Table 8-3

ORIGINS AND HOMOLOGIES OF THE ENTOTYMPANICS

HOLLARD (1864)

reptilian quadratojugal, amphibian quadratomaxillary

FLOWER (1869)

processus tympanicus ossi petrosi

(*Homo*)

PARKER (1886)

tympanic process of basisphenoid (through loss of developmental independence)

(various lipotyphlous insectivores)

WINGE (1895)

detached part of ectotympanic

(*Tupaia* [=*Cladobates*], *Lemur*, *Propithecus*)

WIŃCZA (1896)

annulus tympanicus of anurans

(*Felis*)

VERSLUYS (1898)

quadrate

GAUPP (1905)

Echidna-pterygoid

(*Tachyglossus* [=*Echidna*])

VAN KAMPEN (1905)

mammalian neomorph (caudal entotympanic)

possibly arose through subdivision of tubal cartilage, Reichert's cartilage, or petrosal

entotympanics of different mammals probably homologous

possible cases of *fusion primordiale* in marsupials (CTPP), insectivores (CTPP) and lemurs (petrosal plate)

(representatives of all mammalian orders)

VAN KAMPEN (1915)

derivative of second branchial arch

(*Dasypus* [=*Tatusia*], *Pteropus*)

FAWCETT (1919)

derivative of connective tissue surrounding first branchial pouch

(*Miniopterus*)

..... continued

Table 8-3 -- continued

VAN DER KLAAUW (1922) rostral and caudal entotympanics are new elements unique to mammals rostral entotympanic = possibly a detached portion of tubal cartilage or may be a phylogenetically independent element caudal entotympanic = probably phylogenetically independent of hyoid arch (*Rousettus*, *Pteropus*, *Galeopithecus*, *Dasypus*, *Procavia*, *et al.*)	WEGNER (1942) rostral entotympanic = 'epipterygoid' of monotremes and lower vertebrates caudal entotympanic = new formation of mammals (various mammals, incl. insectivores and primates)
REINBACH (1952) rostral entotympanic = not identical to cartilage of the tube, but formed from same primordium and as a result of the same causes (part of tubotympanic) caudal entotympanic = derivative of second branchial arch (portions of Reichert's cartilage + cornu hyale) (pluripotential fibrous membrane can also produce tympanic processes) (*Dasypus*)	SCHNEIDER (1955) (caudal) entotympanic not necessarily formed from second branchial arch entotympanics of different mammals may not be homologous (*Bradypus*)
LE GROS CLARK (1959, 1971) detached portion of petrosal plate (*Tupaia*, *Lemur*)	SPATZ (1966) unique to mammals in form, function and composition not a derivative of the second branchial arch in every case (rostral) entotympanic may have undergone *fusion primordiale* with tubal cartilage petrosal plate of lemurs produced through *fusion primordiale* of an entotympanic earlier in phylogeny (*Tupaia*)

The forms which led authors to their respective conclusions about the entotympanics are placed in parentheses beneath other entries.

the breadth of forms to be included under the term 'ancient mammals'. Further, it is clear from other contexts that he would have expected the (caudal) entotympanic to have appeared prior to the splitting of the marsupial and placental lineages, if not much earlier. It is worth making some supplementary points respecting these topics.

Entotympanics have yet to be identified in any of the wholly extinct, non-therian mammalian orders (multituberculates, docodonts, triconodonts, symmetrodonts and pantotheres). There are no more than a dozen known basicrania or isolated petrosals of these Mesozoic mammals (KERMACK and KIELAN-JAWOROWSKA 1971); yet even the marvelously preserved crania of the multituberculate species Kamptobaatar kuczynskii and Sloanbaatar mirabilis (KIELAN-JAWOROWSKA 1970) display no indication of having possessed entotympanics or, for that matter, any sort of bony ventral wall. While it is impossible to provide proof, the ventral walls of non-therian mammals were probably composed of membrane alone.

This leaves the therian mammals, but the vital Cretaceous evidence is meagre. The Upper Cretaceous palaeoryctoid Asioryctes definitely lacked an entotympanic; the ventral wall was closed by the ectotympanic alone (KIELAN-JAWOROWSKA 1975). The isolated eutherian petrosals from the Bug Creek Anthills quarry display no sign of facets or articular emarginations which might indicate the presence of entotympanics (see illustrations in MACINTYRE 1972). Nor is there any indication of an entotympanic in the Cretaceous marsupial Didelphodon (CLEMENS 1966). However, there is no need to hypothesize that entotympanics existed in ancient marsupials, since there is no adequate proof that they exist in modern metatherians (contra VAN KAMPEN 1905; see 8.5.4). If these elements are, in fact, absent in all metatherians, then the entotympanics may not be merely a general therian innovation--but specifically a eutherian one.

Contra VAN KAMPEN (1905), the late appearance of the entotympanics during the ontogeny of modern mammals does not constitute unequivocal evidence that they are historically recent innovations in higher vertebrate evolution. One cannot simply assume that the relative order of appearance of structures during ontogeny replicates the sequential order of their appearance during evolution (DE BEER 1958). The entotympanics may well be rather new structures, but this is not demonstrated by the timing of their development in Recent forms.

8.5.4 INCIDENCE OF THE ENTOTYMPANICS IN MODERN MAMMALS

VAN KAMPEN (1905) was the first to attempt a realistic appraisal of the distribution of the entotympanics in modern mammals. His list was slightly modified by his student, VAN DER KLAAUW (1922, 1929, 1930, 1931). A few more additions and deletions, some of which are important, can be made on the basis of evidence accumulated since then.

Any claim that an entotympanic exists in a Recent mammal should be met with a Scots verdict of 'unproven', unless it is accompanied by suitable ontogenetic evidence for the species in question or a closely-related form. However, the rigorous application of this rule would reduce the incidence list to a truly meagre number of entries. Accordingly, in the synopsis presented in table 8-4, I have included

Table 8-4

INCIDENCE OF THE ENTOTYMPANICS IN MODERN MAMMALS

Subclass: PROTOTHERIA		
Order: Monotremata	NO	
Subclass: THERIA		
Supercohort: Marsupialia	?NO	
Supercohort: Eutheria		
Cohort: Edentata		
Order: Cingulata	YES	R,C
Order: Pilosa	YES	C
Cohort: Epitheria		
Magnorder: Ernotheria		
Grandorder: Anagalida		
Order: Macroscelidea	YES	R,C
Order: Lagomorpha	NO	
Magnorder: Preptotheria		
Grandorder: Ferae		
Order: Carnivora	YES	R,C (more than two?)
Grandorder: Insectivora		
Order: Erinaceomorpha	NO	
Order: Soricomorpha	NO	
Grandorder: Archonta		
Order: Scandentia	YES	R or C
Order: Dermoptera	YES	R,C
Order: Chiroptera	YES	R,C
Order: Primates	NO	
Grandorder: Ungulata		
Order: Tubulidentata	NO	
Order: Artiodactyla	?NO	?
Order: Cetacea	NO	
Order: Perissodactyla	?YES	?
Order: Hyracoidea	YES	R,C
Order: Proboscidea	?NO	
Order: Sirenia	?YES	?
Magnorder: ?Preptotheria *incert.sed.*		
Order: Pholidota	YES	C
Cohort: Epitheria *incert.sed.*		
Order: Rodentia	NO	

NO = absent; YES = present; ?NO = unknown, probably absent; ?YES = unknown, possibly present; R = rostral entotympanic; C = caudal entotympanic probable cases as well. The classification outline presented in the table is abstracted from MCKENNA's (1975) recent scheme. I have used it not because it is necessarily better than other classifications, but because I have certain comments to make about his taxonomic location of primates.

The notes in the following paragraphs are principally concerned with the discussion of new evidence on the distribution of entotympanics which has come to light since the publication of VAN DER KLAAUW's (1931) major work.

Although several authors (VAN KAMPEN 1905; VAN DER KLAAUW 1931; DE BEER 1937) have mentioned in passing that an entotympanic might occur in monotremes, the evidence is against this. The elements are definitely absent in *Tachyglossus* (KÜHN 1971). The status of *Ornithnorhynchus* is still uncertain.

It is incredible that not a shred of good embryological evidence has ever been produced to substantiate VAN KAMPEN's (1905) assertion that a (caudal) entotympanic occurs in many marsupials (see 8.5.5). Since there appear to be no new data on the supposed metatherian entotympanic, I have placed a '?NO' next to Marsupialia in the table. I suspect that the question mark is unneeded.

There is excellent embryological evidence for the presence of entotympanics in both cingulates and pilosans, even if there are difficult problems in their interpretation (VAN KAMPEN 1915; VAN DER KLAAUW 1922; REINBACH 1952; SCHNEIDER 1955). For this reason, I am disposed to accept VAN DER KLAAUW's (1931) contention that the entotympanic elements are widely distributed among edentates and may in fact be of universal or nearly universal occurrence in that group. Considering the diversity of forms enclosed within this cohort, however, better evidence is required for some families (particularly Myrmecophagidae) before the latter claim can be made.

The epitherians display wide diversity, as the table illustrates. Both entotympanics are present in living macroscelideans (VAN DER KLAAUW 1929; this study), but they appear to be wholly absent in lagomorphs (see HOYTE 1961).

STARCK's (1964) and HUNT's (1974) recent investigations, combined with evidence in the older literature, establish that entotympanics occur in all major families of carnivores. It was previously believed that some arctoids, particularly ursids, lacked these elements. HUNT's (1974) discovery that up to three separate entotympanics occur in carnivores may be a further indication that these elements have been separately invented several times.

No investigation has ever revealed an independent entotympanic in the Lipotyphla. The only family which is still of doubtful status is Chrysochloridae. FORSTER COOPER (1928) mentions that a small ossicle, the 'eustachian cover', conceals the pharyngeal aperture of the tubal foramen in several species of Chrysochloris. I have found this structure in adults of Carpitalpa (=Chlorotalpa) stuhlmanni; it may simply represent a highly calcified tubal cartilage, although it seems to be bony. The element has not been identified in any of the relevant studies of young stages of golden moles (BROOM 1916;

ROUX 1947; SIMONETTA 1957c and pers. comm.). If the 'eustachian cover' is a rostral entotympanic, its position is unusual in that it lies exterior to the bullar wall *per se*.

Embryological studies have shown that one or the other, or both of the entotympanics occur in Scandentia (SPATZ 1966), Dermoptera (VAN DER KLAAUW 1922, 1930), and Chiroptera (FAWCETT 1919; VAN KAMPEN 1905; VAN DER KLAAUW 1922; FRICK 1954). Adult studies (VAN KAMPEN 1905; VAN DER KLAAUW 1931) indicate that entotympanics are probably constant among all members of these three orders. They are not always fully ossified in megachiropterans and the (?rostral) entotympanic of Tupaiinae may not be the equivalent of the (?caudal) entotympanic of *Ptilocercus*.

STARCK (1975) has recently maintained that an entotympanic may be present in *Tarsius*, on the ground that cartilage can be found in the developing bulla of young *T. bancanus*.[1] He does not indicate whether this cartilage is independent of the rest of the bulla, however. I suspect that the material he identifies as possibly entotympanic in origin is either part of a well-developed CTPP or secondary cartilage in the growing petrosal plate (cf. conditions in lemurs, 2.1.3). All other lines of evidence are heavily in favor of the proposition that entotympanics are absent in modern primates.

The incidence of the entotympanics in the ungulate orders is very uncertain. Only hyracoids have been properly investigated

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[1] WÜNSCH (1975), who has studied the same material, concludes that an entotympanic cannot be discriminated.

(VAN DER KLAAUW 1922, 1930). It is seemingly absent in elephants and whales. Supposed instances of the entotympanics in artiodactyls, perissodactyls and sirenians are based on extremely poor evidence.

There appear to be no exceptions to the rule that the entotympanics are absent in rodents (VAN DER KLAAUW 1931). WEBSTER's (1966) statement that there is an entotympanic in kangaroo rats is incorrect (see WEBSTER 1975).

8.5.5 OF ENTOTYMPANICS, LOST AND GAINED

Table 8-3 shows that there has been no dearth of attempts to derive entotympanics from structures other than the tubal cartilage or the second visceral bar. In particular, a number of authors have viewed the tympanic processes in other basicranial bones as suppressed entotympanics. Each case must be considered on its own merits, and I will not categorically state that suppression of this sort has never occurred. However, my own researches lead me to believe that entotympanic suppression must be a very rare event, and it should not be presumed to have occurred in order to avoid difficulties.

Two instances of supposed suppression are evaluated here. The first concerns the proposition that the petrosal plate of primates is the equivalent of the entotympanic of tupaioids, but has lost its developmental independence. However, discussion is not limited to this topic alone, since there are other alternatives which must be considered. The second concerns the notion that the CTPP of marsupials and lipotyphlans was once an entotympanic, but now appears as an outgrowth of the petrosal.

The Primate Petrosal Plate

Virtually all of the significant research on the tupaioid auditory region has been carried out within the context of the larger debate concerning the mutual affinities of the tree shrews and primates (especially the lemuriform primates). In consequence, structures considered to have special relevance to the confirmation or denial of tupaioid membership in the primate order have received an extraordinary amount of attention over the years. This is particularly true of the bony floor of the middle ear: the bullae of adult tree shrews and primates are clearly and remarkably similar in a number of respects, a point which has been made even by those who would deny primate status to the tupaioids (MCKENNA 1966; VAN VALEN 1965).

However, while similarities exist, so do pronounced differences. The difference which has proven the most troublesome is the contrast the two groups display in bullar construction. The bulla of tree shrews is a compound structure, for there is in addition to the entotympanic a minute CTPP (SPATZ 1966). The lemuriform bulla, on the other hand, is formed by outgrowths of the petrosal alone. Thus, in the former group there are two ossifications contributing to a structure which is formed by a single ossification in the latter. Because of the weight given basicranial characters, this might be construed as a fundamental difference which blocks any close association of tree shrews and primates. The task of those supporting a proximate relationship between tree shrews and primates has been, and still is, to suggest mechanisms which could have produced so marked a difference in the method of middle ear enclosure.

DE BEER (1937:504) has shown that there are four logical possibilities, of which suppression is only one, which can explain why similar positions can be occupied by two bones in one form and only one in another. No single author has systematically reviewed these interpretive alternatives or considered their relative merits as they relate to the tupaioid entotympanic and primate petrosal plate. The four positions can be briefly outlined as follows, along with the substantiating arguments of their major supporters.

(1) Non-homology of the entotympanic and the petrosal plate

The first possibility is that the tupaioid entotympanic and primate petrosal plate are simply non-homologous. That is, they have had entirely separate evolutionary origins and the gross similarities of the tupaioid and lemuriform bullae are due to convergence.

The necessary corollary to this argument is that the entotympanic was never present in primates sensu stricto. SZALAY (1972a, 1972b) has recently confirmed that no fossil primate shows any evidence of an entotympanic element. It must be admitted that the number of early Tertiary primate fossils with preserved basicrania is small, but existing data indicate that a petrosal bulla is an ordinal characteristic of primates. VAN VALEN (1965), in a study of the bullae of contemporary prosimians and tupaioids, concluded that there is no strong evidence of homology.

(2) Fusion primordiale of the entotympanic and petrosal (suppression)

VAN KAMPEN (1905) was struck, as many others have been, by the resemblance of the tupaioid bulla to that of lemurs. Although what ontogenetic evidence there was at his time indicated that the lemuriform bulla probably developed as an outgrowth of the petrosal, he (1905:366, 680-681) thought it likely that the petrosal plate was in fact derived from an eneotympanic which had lost its developmental independence at some point in the evolution of lemurs. It remained to detail a process which could account for this loss of independence, and VAN KAMPEN appealed to the notion of fusion primordiale (suppression of developmental independence). SPATZ (1966) supported fusion primordiale for similar reasons.

(3) Division primordiale of the petrosal (subdivision)

LE GROS CLARK's (1971:134) position was never fully adumbrated, but he was aware of the great difficulty in assuming a thoroughgoing homology of the entotympanic and the petrosal plate:

> The osseous bulla [of tupaioids] is formed developmentally from a bony element which has a separate centre of ossification, the entotympanic, but, though such an interpretation has been disputed, it seems probable that this is to be regarded as an extension of the petrous bone which has secondarily acquired a developmental independence.

LE GROS CLARK knew from VAN KAMPEN's (1905) work that the entotympanic was separately ossified in tree shrews, but his conclusion--that the entotympanic was the result of division primordiale--is the reverse of VAN KAMPEN's view and may derive from GREGORY's (1910:274) misinterpretation of the former author (see VAN DER KLAAUW 1931:268).

(4) Entotympanic lost and functionally replaced by the petrosal plate

A final possibility is that the entotympanic was present in early primates (or their immediate forebears), but that it was completely lost and replaced by the petrosal plate. This view has been taken by MCDOWELL (1958), MARTIN (1968b), MCKENNA (1966) and GINGERICH (1976). MCKENNA (1966:12) stated, in a discussion of the leptictid ear region, that:

> Prior to ossification, fusion of the entotympanic to the petrosal [in leptictids] could have led directly to the morphology that came to characterize the primate bulla in the early Tertiary, or the entotympanic cartilage may have simply given way to a descending wing of the petrosal. Ontogenetic evidence from lemurs and lorises favors the second alternative, so that it appears that a basic difference in the mode of bulla formation between primates on the one hand and tupaiids and leptictids on the other dates back at least to the beginning of the Tertiary.

I do not know whether MCKENNA would still make the same argument. In 1966 he saw the leptictids (_sensu lato_) as the forebears of plesiadapiformes, but he (1975:32) now views them as members of his highly-diverse ernotheres.

What forms of evidence would permit an informed choice between these alternatives? In previous pages all the relevant data relating to embryological, paleontological and neontological matters have been presented, and it is from these that we must construct an answer.

Any argument based on _fusion_ or _division primordiale_ is suspect, for the reason that in reptiles and mammals alike change in the number of elements was generally brought about by the loss of some bones and the extension of others (DE BEER 1937). I have already discussed the suppression problem as it affects lemurs (see 2.1.3.3). Simply stated, secondary cartilage in the petrosal plate of developing lemurs is more easily explained as a functional adaptation to rapid growth, and not as the rudiment of a suppressed entotympanic. Neither paleontology nor neontology support the idea that an entotympanic ever existed in true primates. For similar reasons, I reject subdivision. Embryologically, the entotympanic of Tupaia develops like that of many other mammals, i.e., endochondrally and within the fibrous membrane. The petrosal plate of lemurs develops periosteally (except for the cartilaginous precursor of the CTPP) and outside the fibrous membrane. If LE GROS CLARK were right, I would expect, at the very least, that the tupaioid entotympanic would develop intramembranously. Also, it is worth mentioning that petrosal outgrowths (except the CTPP, discussed below) are not at all common among mammals, despite the impression given by LE GROS CLARK's statements. If they were, and entotympanics were not, there might be some reason to believe that the latter are derived from the former. Since the reverse is the true case, division primordiale lacks any support and must fall.

This leaves non-homology and loss as methods of explaining the observed differences in bullar construction. In one sense, they differ only in the matter of degree and where to draw ordinal boundaries, for loss presupposes non-homology. What is really at issue here is what conditions were like in the ancestors of primates and tree shrews, no matter how remote in time those might be.

One can take two (non-exclusive) approaches to the problem of deriving ancestral conditions. First, the fossil record pertinent to the groups in question can be examined. Secondly, surviving groups related to the ones of interest can be scrutinized for primitive vs. derived character states. There is no basicranial evidence for the groups which gave rise to primates and tree shrews, although no one disagrees that the last common ancestor must have lived in the Cretaceous. SZALAY (1975) now locates the ancestors of primates among adapisoricids. Since these forms are also related to erinaceomorphs in his opinion, one could speculate that the adapisoricid ventral wall would have been at least generally similar to that of mid-Tertiary to Recent hedgehogs. Now, what hedgehogs and primates have in common are large petrosal plates and no entotympanics. If this were also the case in the precursors of primates, then the non-homology argument would receive support. That is, if the entotympanics were absent in the ancestors of the primates, the derived condition of the first primates (relative to the presumed erinaceomorph morphotype) would have simply been a further increase in the size of the petrosal plate (and loss of the tympanic process of the basisphenoid, but that is another problem).

The alternative possibility is that the immediate ancestors of primates possessed an entotympanic, and that the derived condition of the original primates was one of loss of this entotympanic and its replacement by a petrosal plate. The erinaceomorph morphotype argument outlined above goes against this, but there are other types of pertinent evidence, such as conditions in modern mammals with imputed ties to primates. MCKENNA's (1975) grouping of primates, flying lemurs, bats and tree shrews in Archonta is of interest here (see table 8-4). _Contra_ MCKENNA (1975:39), tupaioids (or scandentians, to use his term) do not depart significantly from bats and flying lemurs in possessing an entotympanic. The embryological evidence demonstrates that _both_ entotympanics exist in chiropterans and dermopterans (see 8.5.2). It is the primates, not the tree shrews, which differ from all other archontans. I will not tranduce the Hennigian purity of MCKENNA's classification by talking about 'ancestors', but since he does not discuss the cladistics of this matter I will do it for him. Whether one takes tree shrews, bats or flying lemurs as the sister group of primates, the autapomorphy of primates must be the loss of one or both of the entotympanics and its replacement by petrosal outgrowths. Indeed, things are a bit easier with tree shrews, since one need consider the loss of only one entotympanic.

As the evidence stands, it is a matter of choice as to which of the two more likely possibilities one chooses. On the whole, I favor the non-homology argument, since I see no reason for supposing that the entotympanics have ever figured in primate ancestry. With some violence to NEWTON, _non_ _fingo_ _ossa_---I posit no bones.

The Caudal Tympanic Process of the Petrosal

The data on the ontogeny of the CTPP presented in previous chapters establishes that this process arises and ossifies in continuity with the rest of the auditory capsule. The few sufficiently detailed references in the literature to the CTPP (not always identified as such) agree with these findings (VAN DER KLAAUW 1922, 1929, for Rousettus and macroscelideans; DE BEER and WOODGER 1930, for Lepus; STARCK 1941, for Manis; ROUX 1947, for Suncus). Accordingly, I conclude that the CTPP can be legitimately regarded as a true outgrowth of the auditory capsule, as it never shows any sign of independent existence.

I also reject, as unproven, VAN KAMPEN's (1905) contention that the CTPP of certain marsupials and insectivores represents a suppressed entotympanic. Although he is cited as the authority for the presence of the (caudal) entotympanic in Didelphidae, Peramelidae, Dasyuridae and Macropodidae (e.g., SEGALL 1969a, 1969b, 1970), he did not demonstrate its developmental independence in a single case. Instead, he relied on the observations of HYRTL (1950) and PARKER (1886) concerning independent elements, despite the fact that he often had cause to reject the findings of these authors in other contexts. In all of the marsupials available to VAN KAMPEN the 'entotympanics' of HYRTL and PARKER were continuous with the petrosal or other basicranial bones. Yet he nonetheless concluded that sutural obliteration must have taken place in some cases and fusion primordiale in others.

Now, in order for an hypothesis of fusion primordiale to have any credence in this instance, it must be possible to demonstrate that an entotympanic does, in fact, exist in some marsupials or in their definite ancestors. Otherwise, there is no particular reason for regarding the CTPP as a suppressed entotympanic, since it could as easily represent a true outgrowth of the petrosal. The surprising thing is that the developmental independence of the so-called marsupial entotympanic has not yet been embryologically demonstrated in a single case, more than seventy years after the publication of VAN KAMPEN's (1905) monograph. It seems to me that the whole notion that the entotympanic is widely distributed among marsupials requires a thorough investigation using the correct techniques, since I deduce from existing descriptions that what authors have called the entotympanic is simply an enlarged CTPP (or, in some cases, perhaps a RTPP as well).

The insectivore evidence is even less compelling and does not require discussion. Essentially, VAN KAMPEN (1905) suggested that the enlarged CTPPs of some lipotyphlans may be entotympanics entirely on the ground that they conform in position to the equivalent outgrowths of marsupials. Since it is doubtful that the marsupial CTPP is a suppressed entotympanic, there is no reason to suspect that the lipotyphlan CTPP is other than what it appears to be. VAN DER KLAAUW (1931) reached the same conclusion on the footing that both rostral and caudal entotympanics and the CTPP exist in some mammals.

8.5.6 SUMMARY

In previous chapters, the terms 'rostral entotympanic' and 'caudal entotympanic' were used as though their origins and homologies in different mammals were definite and unquestionable. This is far from the actual case, as I have tried to show here.

At the same time, several controversial problems surrounding these peculiar elements are clearer in my own mind, if not actually solved. Other students may care to differ with me over some of my interpretations, but I have attempted to be evenhanded in the presentation of data and conflicting arguments. In any event, it is my opinion that:

(1) the entotympanics should be considered eutherian neomorphs, pending a convincing demonstration of their presence in extinct mammals without modern issue, monotremes and marsupials. Evidence relating to the last group would be particularly easy to acquire, and ought to be gathered in the near future;

(2) to the extent that the concept of the 'morphotype' has some utility in paleontology and taxonomy, the presence of an entotympanic may be made part of the eutherian morphotype. This is primarily suggested by the wide distribution of entotympanics in modern mammals, not by the poor amount of fossil evidence. No doubt cladists will find it particularly interesting that entotympanics are probably universal in edentates, but are reduced or lost in many epitherian orders. It is also worth noting, in this connexion, that the most primitive form of the entotympanic (according to VAN DER KLAAUW 1931) is a small, pyradmidal plate lying behind the auditory tube and grooved by a sulcus for the (medial) carotid artery. This condition is found in Cingulata, Pilosa, Pholidota (VAN DER KLAAUW 1931) and Carnivora (HUNT 1974).

However, I hesitate to specify which of the entotympanics should be included in the morphotype. The entotympanic bearing the carotid sulcus is the caudal entotympanic in pilosans and the rostral entotympanic in carnivores. Furthermore, overhanging any ascription of an entotympanic to the eutherian morphotype is the prior problem of the equivalency of the entotympanics in different mammals generally. That independent chondro-osseous elements have long been associated with the eutherian ventral wall is unquestionable; whether these are all of the same value is a different question without a suitable answer at present;

(3) there is no compelling reason to believe that entotympanics in the suppressed state exist in Recent primates or lipotyphlans. Parsimony is on the side of the argument that entotympanics did not exist in the immediate ancestors of primates either. Yet much depends on the latitude one gives to the term 'basal primates'. (If microsyopids are members of this group, as GINGERICH (1976) has recently argued anew, then the entotympanic must have been lost in the line leading to modern primates.) This applies _a fortiori_ to the term 'stem lipotyphlans'. Several early Tertiary groups, which have been imputed to have 'insectivore' ties at one time or another, possess an entotympanic (e.g., Leptictidae, Microsyopidae). Modern scholarship, however, suggests these ties are illusory (SZALAY 1969; BUTLER 1972; MCKENNA 1975).

8.6 CONCLUSION: INTER-TAXON COMPARISONS

The inter-taxon comparisons reported in this final section are not meant to serve as taxonomic discussions, but simply as vehicles for placing important findings in an appropriate context.

8.6.1 LEMURIFORMES AND LORISIFORMES

It is increasingly apparent to students of strepsirhine taxonomy and evolution that the scale of anatomical differences between lorises and lemurs has been overstated (see, in particular, CARTMILL 1975). In the case of the auditory region, overstatement has taken the form of defining sharp contrasts where few exist and citing characters individually without taking into account their possible degrees of correlation. Furthermore, some of the sharpest distinctions made in the literature are simply invalid, for they are based on misevaluations of homologies. Findings from my ontogenetic investigations which are pertinent to these matters are the following:

(1) Origin of the Bulla

The petrosal plate has the same origin in both strepsirhine groups, despite evident differences in the form of the bulla in adult stages. Neither group possesses an entotympanic, and the petrosal plate arises from both an RTPP and a CTPP. Indeed, prior to the onset of the pneumatization process there is little which distinguishes the developing bullae of lorises and lemurs.

This early similarity is to be expected, and no undue importance should be attached to it. Early bullar ontogeny is evidently similar in both strepsirhines and *Tarsius*, judging from the descriptions and illustrations in the publications of STARCK (1975) and WÜNSCH (1975). The distinctive form of the CTPP separates strepsirhines from all other groups considered here; it remains to be seen, however, whether this is a general trait of all primates.

(2) Patterns of Pneumatization

This study has detailed the profound effects of pneumatization on the anatomy of the strepsirhine middle ear. The extent to which pneumatic activity provides the major shaping influence on several of the taxonomically-significant features of the basicranium has not been adequately recognized in other studies.

Briefly, the lorisiform pattern of pneumatization is characterized by early, intense activity in the central and posterior parts of the dorsal wall. Air-spaces rapidly spread from there into the greater part of the petrosal, including the petrosal plate. Conversely, the intratympanic face of the ventral wall is not an important site of pneumatization, and a true hypotympanic sinus is barely indicated in adult lorises.

In lemurs, the pattern of pneumatization is effectively the reverse of that found in lorises. The ventral wall is strongly affected by pneumatization, thus producing a capacious hypotympanic sinus. The epitympanic recess must be considered large, but the mastoid and supracochlear cavities are insignificant in most species.

These two patterns are graphically illustrated in fig. VIII-2. The arrows indicate, in a rough way, the major trajectories of pneumatic activity and the relative positions of the principal spaces in the adult stage.

Correlated with the lorisiform pattern of pneumatization are the following features: the medial accessory cavity, the lateral lamella of the petrosal plate, the posteromedial position of the posterior carotid foramen, and the phaneric condition of the ectotympanic. Correlated with the lemuriform pattern of pneumatization are: a large hypotympanic sinus, a shield-like posterior septum, the posterocentral or posterolateral position of the posterior carotid foramen, and the aphaneric condition of the ectotympanic. A knowledge of how pneumatization affects the production of each of these features permits the following series of conclusions:

(i) The medial accessory cavity of lorises is not formed in the same way as the hypotympanic sinus of lemurs, and should not be called by the same name. The medial accessory cavity emerges as one of the hallmarks of the lorisiform auditory region, for it can be detected in the earliest known undoubted lorises (WALKER 1974). This space is not possessed even by Cheirogaleus (=Allocebus) trichotis, considered to be the most loris-like of Recent lemurs by CARTMILL (1975).

(ii) The lateral lamella of the petrosal plate of lorises is not the equivalent of the anterior (principal, longitudinal) septum of lemurs, and all comparisons between them are analytically meaningless. This feature is also characteristic of ancient lorises (WALKER 1974) and does not exist in any known modern or fossil lemurs. Note, however, that it is tautological to consider it as a character separate from the medial accessory cavity, since it is produced by the expansion of the latter into the substance of the petrosal plate.

The shield-like posterior septum of lemurs is not a 'reduced' or an 'incipient' lateral lamella according to my analysis. Unlike the former, it is produced by the sculpturing effects of pneumatic activity within the true hypotympanic sinus.

(iii) In lemurs, the placement of the posterior carotid foramen is partly determined by the extent of pneumatization in the posterior part of the middle ear. In lorises, the internal carotid artery is entrapped by the material of the petrosal plate early in bullar ontogeny, and the resulting foramen is not thereafter appreciably affected by pneumatization. Entrapment occurs relatively much later in lemurs. Further, it should be noted that the posterior carotid foramen of lorises is actually located far back on the bullar wall (fig. III-2). It appears to occupy a central position because of the massive size of the mastoid cavity.

(iv) Sutural tissues play the major role in determining the final form of the ectotympanic-petrosal plate relationship. In lemurs, pneumatization affects the condition of the relationship to some extent. In lorises, however, its role is negative, since there is no significant swelling of the ventral wall.

The principal reason for organizing these findings around the effects of pneumatization is to illustrate how important this process is to the evaluation of correlations between characters. Strepsirhine taxonomy would be well served if, in future, workers pay due attention to the consequences of pneumatic activity on bony form.

(3) Carotid System

My findings contribute little that is not already discussed in CARTMILL's (1975) thorough evaluation of the carotid system in strepsirhines. The only matter about which I am hesitant is his speculation that an anastomosis of the ascending pharyngeal and circulus arteriosus may be a transitory development in young stages of most placentals, let alone non-cheirogaleid lemurs. Only further investigations can solve this highly-important puzzle.

Since all lemuriform primates share a similar pattern of pneumatization, and since the traits correlated with this pattern characterize all members of this infraorder, I cannot support the inclusion of cheirogaleids in Lorisiformes (cf. TATTERSALL and SCHWARTZ 1974). Patterns of pneumatization deserve a high weight in this instance, since they are, in fact, sharply different in the two strepsirhine groups and not merely due to the cessation of an ontogenetic process in the one and its continuance in the other (see CARTMILL's [1975] analysis of the ascending pharyngeal-circulus arteriosus anastomosis and the relationship of the ectotympanic to the petrosal plate).

8.6.2 STREPSIRHINI AND TUPAIOIDEA

The auditory region of tupaioids was formerly regarded as one of the strongest indicators of close ties with lemuriform strepsirhines (e.g., LE GROS CLARK 1925, 1959, 1971). With a few exceptions (e.g., SABAN 1956-57), modern opinion takes the reverse stand (e.g., VAN VALEN 1965; SZALAY 1972b); the auditory region is now commonly employed to show that close ties are illusory. The weight of the ontogenetic and microanatomical data presented here supports this latter view.

Two characters of the tupaioid and lemuriform auditory regions have occupied the center of the conflict over tupaioid affinities. These are the aphaneric condition of the anular ectotympanic, and the form and constitution of the auditory bulla. In respect of the aphaneric ectotympanic, ontogenetic investigation establishes fairly clearly that tree shrews and lemurs arrive at identical character states through very different means. In tree shrews, the entotympanic has no primary relationship with the ectotympanic at all, and enclosure is essentially a passive process. In lemurs, the relationship is far more intimate, although the end result is the same. The petrosal plate meets the ectotympanic as it grows along the fibrous membrane. But instead of ceasing growth or fusing with the ectotympanic (as in lorises), the petrosal plate grows around it because no sutural tissues are elaborated at the interface. To me, this indicates convergence rather than synapomorphy in the style of ectotympanic enclosure.

The second character, the nature of the bulla, is more difficult to evaluate. It is evident from the ontogenetic data that the petrosal bulla of lemurs develops very differently from the entotympanic one of tree shrews. Although various arguments can be advanced for the propositions that the bullae of these two groups have undergone various secondary modifications which conceal their homology, I do not find the evidence for these views very convincing. It is surely also important that an entotympanic has never been positively identified in any fossil primate (SZALAY 1972a, 1972b).

Other similarities in the construction of the auditory regions of strepsirhines and tupaioids have often been overemphasized (see VAN VALEN 1965). It is true that Tupaiinae lack tympanic processes of the basisphenoid and the alisphenoid, but the latter is certainly present in Ptilocercus. There is in fact a very well-developed epitympanic wing of the sphenoid in all tree shrews, but this is covered in the adult by the dorsal part of the entotympanic, The general similarity in septal content is of minor interest, especially when it is noted that the septa develop in different ways from different elements. The ramus inferior is not completely absent in tree shrews, and even if it were this would not be a unique resemblance to primates. Certain tenrecs also lack this vessel. The examples could be multiplied, but I think the point is clear. Sufficiently-detailed analysis of the characters that are supposed to demonstrate strong ties between primates and tree shrews are either not clear-cut or can be validly regarded as convergences or primitive retentions.

8.6.3 STREPSIRHINI AND OTHER GROUPS

It is now necessary to evaluate the basicranial evidence for the degree of relationship between primates, macroscelideans and lipotyphlans.

The case of the elephant shrews does not merit extensive discussion. Although macroscelideans and primates have been compared from time to time (see review of the literature in PATTERSON 1965), the auditory region has never played more than a minor role in these investigations.

It is worth underscoring the fact that macroscelideans stand apart from all other mammals in the structural complexity of the ventral wall of the middle ear. This alone makes any meaningful comparison between elephant shrews and other placentals extremely difficult. For example, elephant shrews possess the largest petrosal plate of any non-primate investigated here. Yet it is hard to place much weight on this, since (in contrast to primates) they also possess substantial outgrowths from most other bones of the basicranium. If the axiom is true that tympanic processes are rarely gained or lost, the split between elephant shrews and primates must be ancient indeed. Furthermore, close study of the macroscelidean petrosal plate establishes that it differs from that of primates in at least one important aspect. The caudal tympanic process of the petrosal is like that of other (primitive) mammals, not like that of primates. Similarities in their petrosal plates, to the degree that they exist, are best regarded as convergences.

EVANS (1942) claims that the bulla of macroscelideans resembles that of non-Malagasy lemurs (i.e., lorises), but the quoted resemblances are so superficial that they may be safely regarded as irrelevant. All the two groups share are inflated ventral walls and phaneric, semitubular ectotympanics; lorises do not possess an entotympanic, contra EVANS' statement to the contrary. Swollen bullae and laterally-prolonged ectotympanics are extremely common developments among mammals and no indicators of close relationships.

In sum, I can think of no feature of the auditory region possessed by both primates and macroscelideans that is not either primitive for mammals generally or due to convergence. Although the basicranial evidence is thus of a negative quality, it indirectly supports the conclusions of most authorities that primates and elephant shrews are very distantly related (for a recent assessment of the affinities of macroscelideans, see MCKENNA 1975).

It is likely, for a number of reasons which cannot be reviewed here, that primates ultimately stem from animals which could be noncommittally described as 'insectivores'. Much effort has been expended in recent years in attempts to identify which particular stock of insectivores stands in an immediate ancestral relationship with primates. The current favorites, on dental evidence, are late Cretaceous erinaceotans (CLEMENS 1974).

It would be useful if this hypothesis could be corroborated or denied by evidence from some other anatomical system, such as the ear region. However, in my view, our present state of knowledge concerning the basicranium of extinct lipotyphlans is too meagre for positive statements concerning the relationships of particular insectivore families to primates.

Nonetheless, SZALAY (1975:99) claims that "primitive primates share more significant similarities with the erinaceotan (sensu

VAN VALEN 1967) morphotype than with any other group". The latter morphotype is left undefined, and supposed shared characters are discussed in relation to his concept of the primate morphotype only (large petrosal component, no medial carotid, rounded promontory, bony canals for carotid branches, and shield-like posterior septum). Now, it is true that these traits, as defined by SZALAY, can be said to characterize the basicrania of both primates and erinaceotans. However, I suggest that they also characterize soricomorph lipotyphlans to about the same extent (see chapter 7; bony canals for carotid branches are found in chrysochlorids). It is true that no known shrew has so large a petrosal component in the ventral wall as do certain extinct Oligocene-Miocene erinaceids (see GAWNE 1968; RICH and RICH 1971), but it is also true that the other features cited above are found in soricomorphs as well. My point is that it is an excess of refinement to claim that a specific group of lipotyphlans is definitely more closely related to primates than other such groups are--at least on the basis of existing basicranial evidence.

8.6.4 TUPAIOIDEA AND MACROSCELIDEA

Nearly all taxonomic evaluations of tupaioids and macroscelideans made in this century have concluded that the phyletic gulf separating them is extremely wide (LE GROS CLARK 1933; MEISTER and DAVIS 1956; PATTERSON 1965). This is in contrast to formulations like that of HAECKEL (1886), which united them in a single order (Menotyphla).

The classic character of the auditory region which was said to indicate their affinity was the shared presence of an entotympanic (VAN KAMPEN 1905). Not only do elephant shrews differ from tupaioids in possessing two entotympanics (VAN DER KLAAUW 1931), but also differ in the very methods by which those elements are produced during ontogeny. Here, as elsewhere, the simple presence of entotympanics in two groups of mammals is no indicator of their close affinity (see 8.5).

Elephant shrews possess a large tympanic process of the alisphenoid, as does Ptilocercus among the tupaioids. I attach little significance to this, since the same process is commonly present in marsupials and (in a reduced state) in lipotyphlans.

The differences between elephant shrews and tree shrews in the construction of the auditory region substantiate the proposition that they are only distantly related. Among the important features in this respect are the rostral tympanic process of the petrosal (present only in elephant shrews) and the epitympanic wing of the squamosal (present only in tree shrews). Other features merely show that they are both primitive placental mammals (form of the caudal tympanic process of the petrosal, large epitympanic wing of the sphenoid, preservation of the ramus inferior of the stapedial artery).

8.6.5 TUPAIOIDEA AND LIPOTYPHLA

Tree shrews and lipotyphlans (especially erinaceomorphs) share several structural similarities of the auditory region, but all appear to be primitive. Two of the obvious ones are the form of the CTPP and the large epitympanic wing of the sphenoid. The chief specialization of tree shrews compared to modern insectivores is the presence of the entotympanic. It is conceivable that this ossification appeared in the ancestors of tree shrews after they separated from basal insectivores (indeed, without its entotympanic covering the tupaioid auditory region is quite erinaceid-like). However, the lack of any pertinent basicranial evidence from fossils makes this no more than an unsupported speculation.

8.6.6 MACROSCELIDEA AND LIPOTYPHLA

As with tupaioids, there are few characters of the auditory region which elephant shrews and insectivores share that are not primitive. One exception to this statement may be the tympanic process of the basisphenoid, although a competent authority denies that this outgrowth is present in elephant shrews (VAN DER KLAAUW 1931). If macroscelideans have significant phyletic relationships with any contemporary insectivore family, this cannot be deduced from characters of the auditory region.

It may be mentioned parenthetically that it would be hard to argue for meaningful ties between lagomorphs and elephant shrews on the basis of their auditory regions, although MCKENNA (1975) does so for dental features. In contrast to the multiplex bulla of macroscelideans, lagomorphs possess a bulla formed solely by the ectotympanic (see HOYTE 1961). Further, the evidence is good for the proposition that the 'internal carotid' of rabbits and hares is a true medial carotid (BUGGE 1974). MCKENNA's (1975) association of elephant shrews and the Oligocene family Anagalidae makes somewhat better sense, although PATTERSON (1965) argues that such a grouping cannot be defended. Judging from MCKENNA's (1963) re-description of the anagalid auditory region, these ancient mammals had bullae with large ectotympanic and (?caudal) entotympanic components, as in modern elephant shrews. The participation of the squamosal and alisphenoid in the anagalid bulla has not been documented.

8.6.7 ERINACEOMORPHA AND SORICOMORPHA

The development of the lipotyphlan auditory region is inadequately covered in this paper, since only Erinaceidae, Tenrecidae and the unusual genus Solenodon among the diverse membership of this order have been examined in detail. However, a few matters are important enough to warrant mention here.

One finds that in the contemporary taxonomic literature there is now a definite leaning towards the proposition that hedgehog-like and shrew-like mammals can be grouped together into a natural taxon (SABAN 1954; MCDOWELL 1958; BUTLER 1972; MCKENNA 1975). This contrasts with the previous view that Lipotyphla is, and perhaps ought to be, a receptacle for mammals whose structure exhibits numerous placental plesiomorphies but reveals little respecting their larger affinities. However, there is still much disagreement over the placement of certain families within the bounds of Lipotyphla; this particularly applies to Talpidae, Solenodontidae, and Chrysochloridae.

Shared derived characters of lipotyphlous insectivores that are not primitive are now believed to include the absence of a caecum, reduction of the jugal, expansion of the maxilla in the orbital wall at the expense of the palatine, possession of a mobile proboscis, reduced pubic symphysis and the hemochorial placenta (BUTLER 1972). At various times workers have tried to inject into this list (or others like it) various features of the auditory region, such as the presence of the tympanic process of the basisphenoid and epitympanic wing of the sphenoid, loss of the entotympanic(s), retention of the ramus inferior of the stapedial artery, and presence of the caudal tympanic process of the petrosal (VAN KAMPEN 1905; SABAN 1956-57; MCDOWELL 1958). The tympanic process of the basisphenoid is very likely a derived character; the trouble is that it is conspicuously absent (or highly reduced) in many soricomorphs. It is possible, as many think, that the tympanic process appeared in the ancestral line of lipotyphlans, but was later lost in certain families of shrews. However, the hedgehog-shrew split probably occurred in the Paleocene or earlier (BUTLER 1972). Since there are no well-preserved basicrania of any undoubted lipotyphlans from this time period, whether or not this loss occurred remains undocumented. The other features mentioned are either probable placental plesiomorphies or of uncertain accuracy (such as the presumption that stem lipotyphlans had an entotympanic to lose).

I do not know whether the ramus posterior of the stapedial artery is an ancient placental trait, although I suspect that it is. Other features of the lipotyphlan carotid circulation are certainly primitive (BUGGE 1974).

Not having had the opportunity to study young stages of soricids I will not offer an opinion on whether Solenodon is more closely related to shrews than to tenrecs (cf. MCDOWELL 1958). The most important otic feature this genus shares with shrews, as opposed to tenrecs, is the absence of the tympanic process of the basisphenoid. One has to weigh the likelihood of a parallel loss of this structure against the possibility that the dentitions of Solenodon and tenrecs show only convergent resemblances. As with so many questions in the character analysis of lipotyphlans, this problem has no easy answer.

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FIGURES

FIG. I-1 Left auditory region of a hypothetical placental mammal (schematic), prior to the formation of extensive tympanic processes and epitympanic wings (cf. figs. I-2, I-3). Most of the important features and landmarks discussed in section 1.4 are identified, although some (e.g., ectotympanic, cartilage of the auditory tube) have been removed to provide an unobstructed view of dorsal structures. Reichert's cartilage is cut close to its base.

1, anterior basicapsular commissure; 2, remnant of processus alaris, marking division between basisphenoid and alisphenoid; 3, alicochlear commissure; 4, posterior basicapsular commissure.

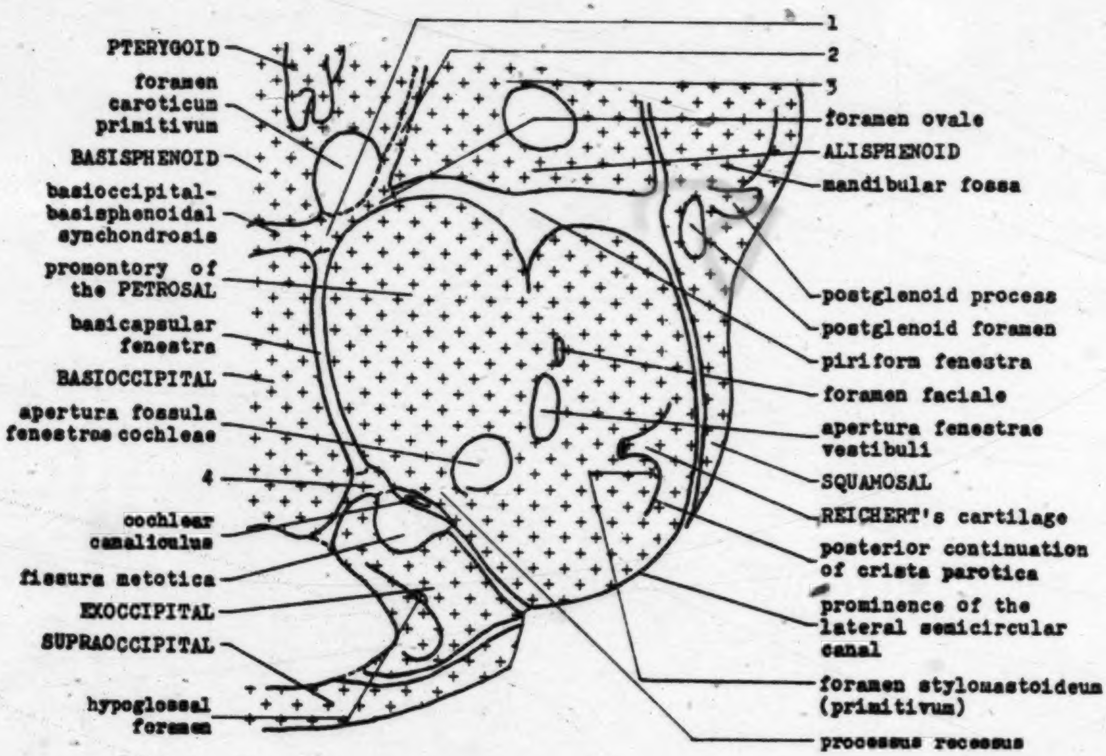

PTERYGOID
foramen caroticum primitivum
BASISPHENOID
basioccipital-basisphenoidal synchondrosis
promontory of the PETROSAL
basicapsular fenestra
BASIOCCIPITAL
apertura fossula fenestrae cochleae
4
cochlear canaliculus
fissura metotica
EXOCCIPITAL
SUPRAOCCIPITAL
hypoglossal foramen
1
2
3
foramen ovale
ALISPHENOID
mandibular fossa
postglenoid process
postglenoid foramen
piriform fenestra
foramen faciale
apertura fenestrae vestibuli
SQUAMOSAL
REICHERT's cartilage
posterior continuation of crista parotica
prominence of the lateral semicircular canal
foramen stylomastoideum (primitivum)
processus recessus

FIG. I-2 Tympanic processes vary greatly in their form and disposition in adult mammals. However, the available sample suggests that there is a good deal of uniformity in the sites of initial origin of these outgrowths. This diagram is a composite; no form investigated here possesses outgrowths at all the sites indicated by stippling. Nevertheless, it reflects with reasonable accuracy those areas which are commonly implicated in the production of tympanic processes, and their relative placement at an early stage of development.

See fig. I-1 for names and locations of other anatomical features. Ectotympanic, entotympanics, and tympanic processes of mammals other than those investigated here are not illustrated.

SF, fossa for stapedius m.; D_3, diverticulum containing saccus posterior of cavum tympani.

1, tympanic process of basisphenoid (sometimes incorporates posterior part of pterygoid)
2, tympanic process of alisphenoid
3, entoglenoid process of squamosal
4, rostral tympanic process of petrosal
5, caudal tympanic process of petrosal, divided into three components:

  5a, medial section
  5b, posterior section
  5c', lateral section, in certain mammals (e.g., tupaioids)
  5c", lateral section, in certain mammals (e.g., strepsirhines)

4 + 5 = petrosal plate

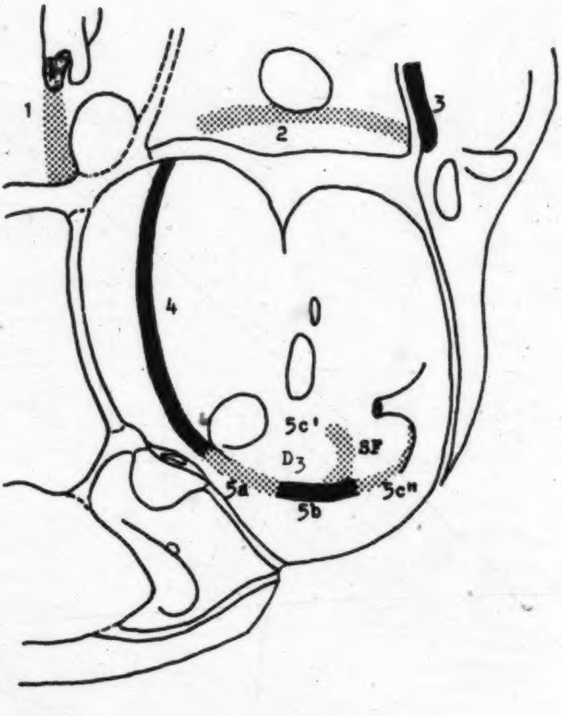

1
2
3
4
5c'
D3
SF
5a
5b
5c"

FIG. I-3 One of the major growth areas of the basicranium is situated along a frontal axis passing through the basioccipital-basisphenoidal synchondrosis and the piriform fenestra. Endochondral growth at the synchondrosis results in the considerable elongation of this part of the basicranium. Accompanying growth occurs along the margins of the piriform fenestra. If growth is sufficient in the latter case, the fenestra will eventually close or reduce to a narrow fissure (petrosphenoid suture); if not, the fenestra will be retained as a ragged breach into adult life.

The pointers indicate directions of growth along the axis described above. No attempt is made to illustrate the growth of the basicranium as a whole.

This diagram is a composite in the same sense as fig. I-2, but section 1.4.2 should be consulted for its proper interpretation. The numbers identify areas of potential growth around the piriform fenestra (see key adjacent to diagram).

1, epitympanic wing of sphenoid (which includes, in many cases, contributions from both the basisphenoid [1a] and alisphenoid [1b]); 2, epitympanic wing of petrosal; 3, tegmen tympani (here depicted as relatively large); 4, epitympanic wing of squamosal.

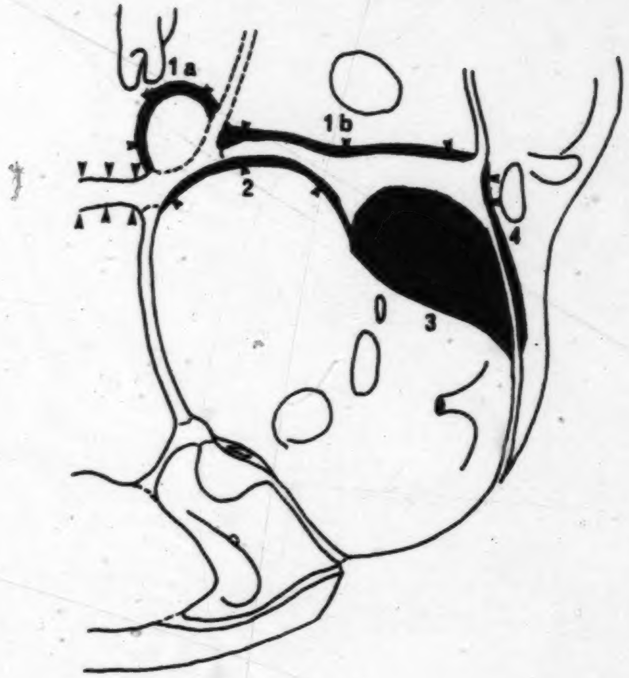

1a
1b
2
3
4

FIG. I-4 Plan of chief arteries and nerves traversing the auditory region of a hypothetical placental mammal. Only major branches and connexions are illustrated. Relative sizes of arteries and nerves are representational only, and no scale is implied. See definitions in appendix II for further information.

1, cerebral carotid a. (in this case, formed by the anastomosis of the anterior carotid and promontorial aa.); 2, branch of internal carotid n., to cavernous plexus; 3, tympanic plexus.

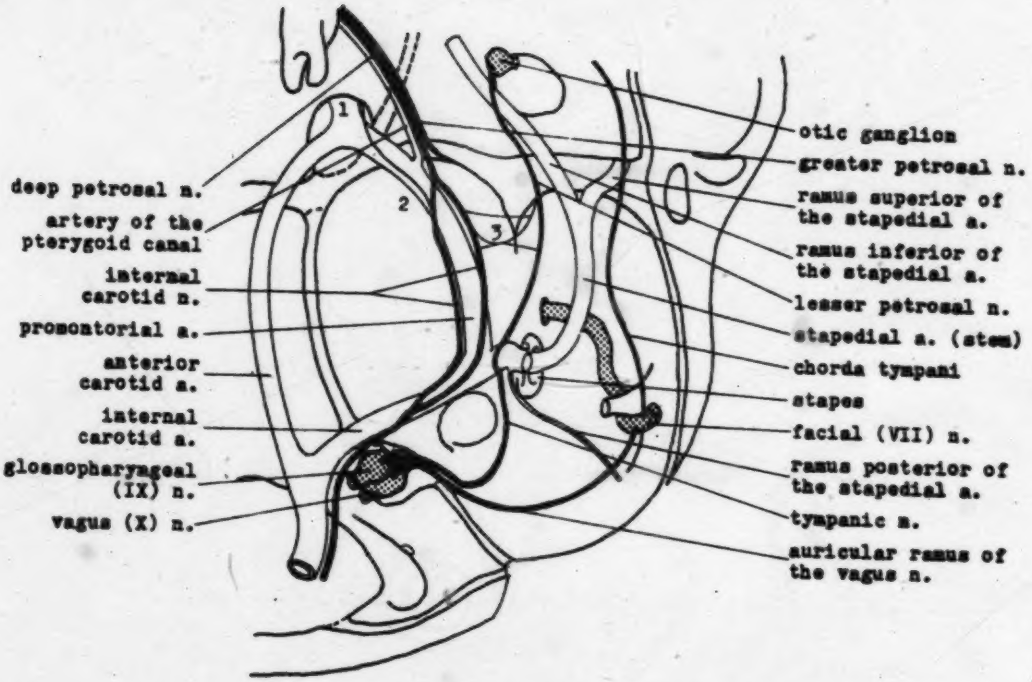

deep petrosal n.
artery of the pterygoid canal
internal carotid n.
promontorial a.
anterior carotid a.
internal carotid a.
glossopharyngeal (IX) n.
vagus (X) n.
1
2
3
otic ganglion
greater petrosal n.
ramus superior of the stapedial a.
ramus inferior of the stapedial a.
lesser petrosal n.
stapedial a. (stem)
chorda tympani
stapes
facial (VII) n.
ramus posterior of the stapedial a.
tympanic n.
auricular ramus of the vagus n.

FIG. II-1 *M. murinus* MPIH 1962/57 (fetus). Reconstruction of left auditory region and associated structures, ca. x 20. Areas marked by widely-spaced dots represent zones of primary cartilage; open circles represent secondary cartilage. Remaining areas are bony.

a. General anatomy.

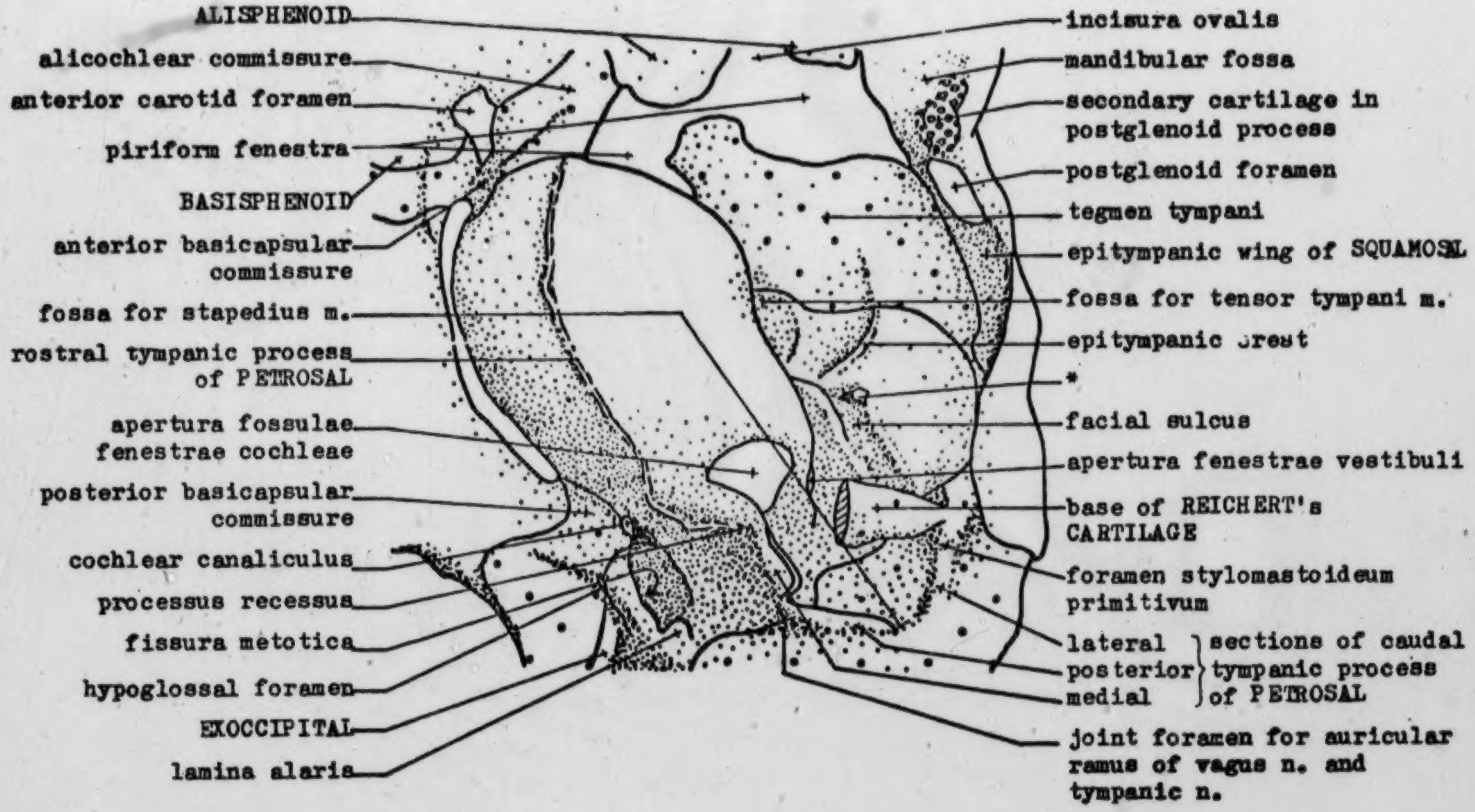
b. Ectotympanic, Reichert's cartilage and the cartilage of the auditory tube *in situ*.

c. Routes of arteries and nerves.

The rostral tympanic process of the petrosal forms an even arc of trabeculae along the middle of the ventral surface of the promontory, directly above the ectotympanic. The caudal tympanic process of the petrosal arises in cartilage in the hind part of the presumptive middle ear. The two processes meet on the processus recessus (medial wall of apertura fossulae fenestrae cochleae).

Parts of the internal carotid n. and a. which would not be visible from this aspect are indicated by dashed lines. Similarly, the anterior part of the tympanic n. has not been drawn in, since the nerve would appear to intersect or overlap the internal carotid n. from this aspect. Despite the appearance given by the drawing, the lesser petrosal n. arises from the tympanic plexus (not visible) as usual, and not from the internal carotid n.

*, foramen for a vein (stapedial a. absent in this specimen; cf. fig. II-2).


ALISPHENOID
alicochlear commissure
anterior carotid foramen
piriform fenestra
BASISPHENOID
anterior basicapsular commissure
fossa for stapedius m.
rostral tympanic process of PETROSAL
apertura fossulae fenestrae cochleae
posterior basicapsular commissure
cochlear canaliculus
processus recessus
fissura metotica
hypoglossal foramen
EXOCCIPITAL
lamina alaris
incisura ovalis
mandibular fossa
secondary cartilage in postglenoid process
postglenoid foramen
tegmen tympani
epitympanic wing of SQUAMOSAL
fossa for tensor tympani m.
epitympanic crest
*
facial sulcus
apertura fenestrae vestibuli
base of REICHERT's CARTILAGE
foramen stylomastoideum primitivum
lateral
posterior
medial
sections of caudal tympanic process of PETROSAL
joint foramen for auricular ramus of vagus n. and tympanic n.

a

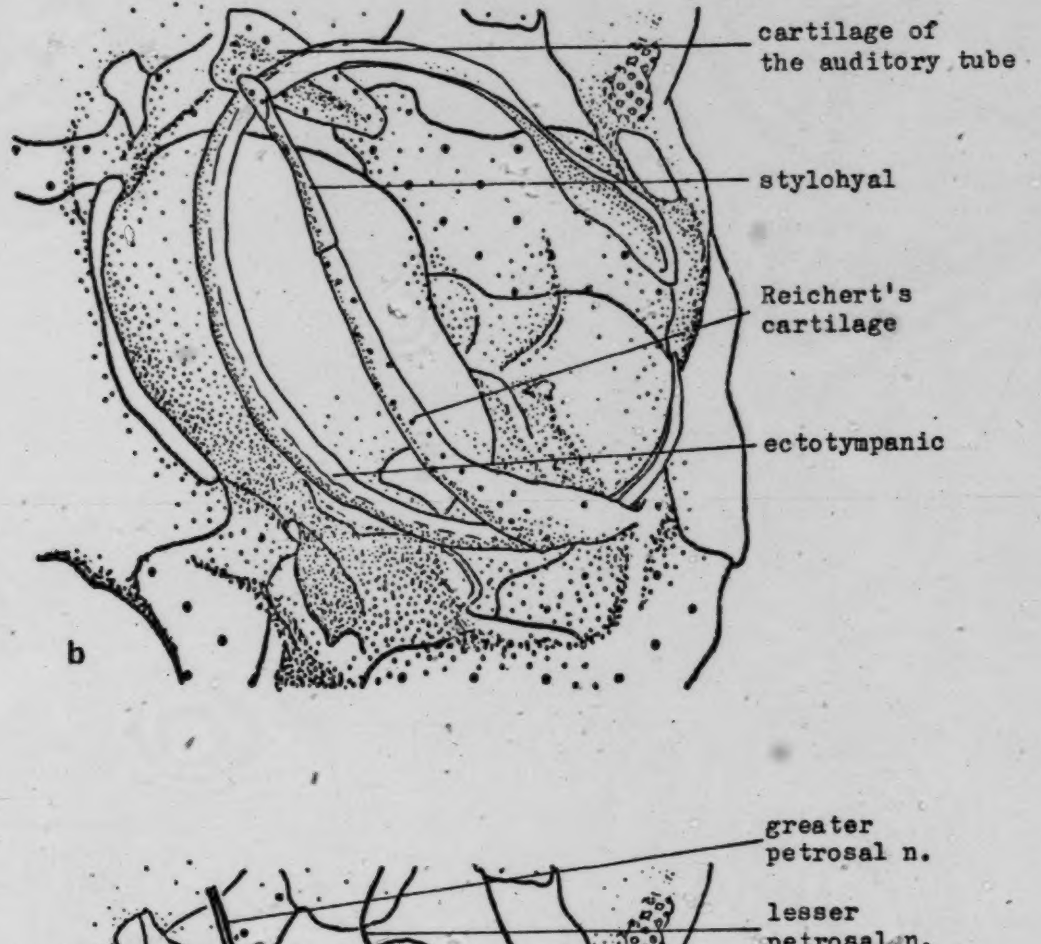

cartilage of the auditory tube
stylohyal
Reichert's cartilage
ectotympanic
b
greater petrosal n.
lesser petrosal n.
chorda tympani
promontorial a.
anterior carotid a.
internal carotid n.
facial n.
ramus auricularis vagi
tympanic n. (to lesser petrosal n.)
c

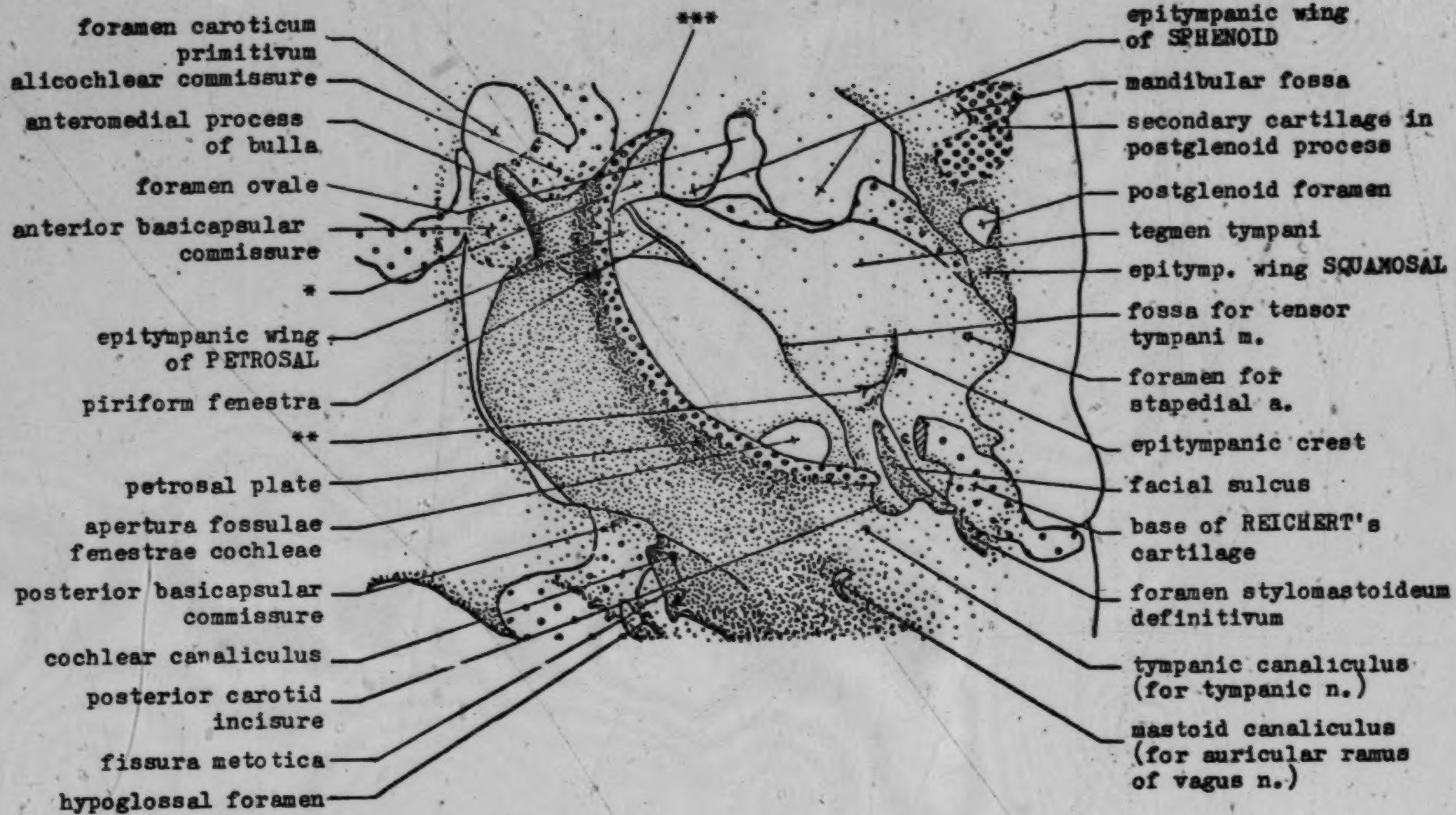
FIG. II-2 M. murinus MPIH 1964/42 (fetus). Reconstruction of left auditory region and associated structures, ca. x 20. See fig. II-1 for shading conventions.

a. General anatomy; ca. x 20.

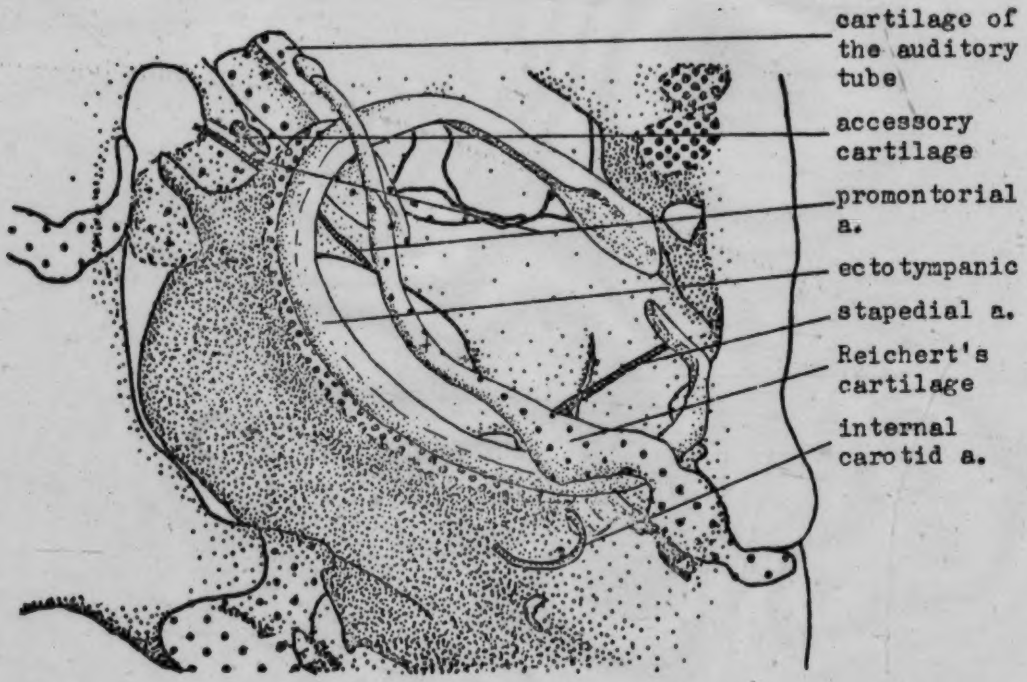
b. Ectotympanic, Reichert's cartilage, and the cartilage of the auditory tube *in situ*; ca. x

The petrosal plate has attained large size and shows some degree of inflation, especially in its anterior part. The rostral and caudal tympanic processes of the petrosal now constitute a single rampart of bone (the petrosal plate). The ectotympanic is still visible, although the extreme anterior end of the petrosal plate is just beginning to overlap it (***). Note the presence of secondary cartilage in the ventral part of the petrosal plate.

Only the divisions of the internal carotid a. are shown in this diagram; for routes of nerves, see fig. II-1. Note that (a) the position of the entry-point of the internal carotid a. into the tympanic cavity has shifted to the posterior relative to conditions in MPIH 1962/57 (fig. II-1); (b) the stapedial a. is present and passes through the epitympanic crest; and (c) the promontorial a. travels along the remnant portion of the piriform fenestra.


foramen caroticum primitivum
alicochlear commissure
anteromedial process of bulla
foramen ovale
anterior basicapsular commissure
*
epitympanic wing of PETROSAL
piriform fenestra
**
petrosal plate
apertura fossulae fenestrae cochleae
posterior basicapsular commissure
cochlear canaliculus
posterior carotid incisure
fissura metotica
hypoglossal foramen
***
epitympanic wing of SPHENOID
mandibular fossa
secondary cartilage in postglenoid process
postglenoid foramen
tegmen tympani
epitymp. wing SQUAMOSAL
fossa for tensor tympani m.
foramen for stapedial a.
epitympanic crest
facial sulcus
base of REICHERT's cartilage
foramen stylomastoideum definitivum
tympanic canaliculus (for tympanic n.)
mastoid canaliculus (for auricular ramus of vagus n.)

a


cartilage of the auditory tube
accessory cartilage
promontorial a.
ectotympanic
stapedial a.
Reichert's cartilage
internal carotid a.

b

FIG. II-3 *L. catta* adult. General view of left auditory region, ventral aspect.

Most of the ventral part of the bulla (petrosal plate) and the ectotympanic have been removed. Note that the massively inflated petrosal plate has migrated medially and no longer occupies the center of the ventral surface of the promontory (see fig. II-2). The posterior septum, however, occupies the position of the original caudal tympanic process of the petrosal.

*, posterior diverticulum of the hypotympanic sinus.

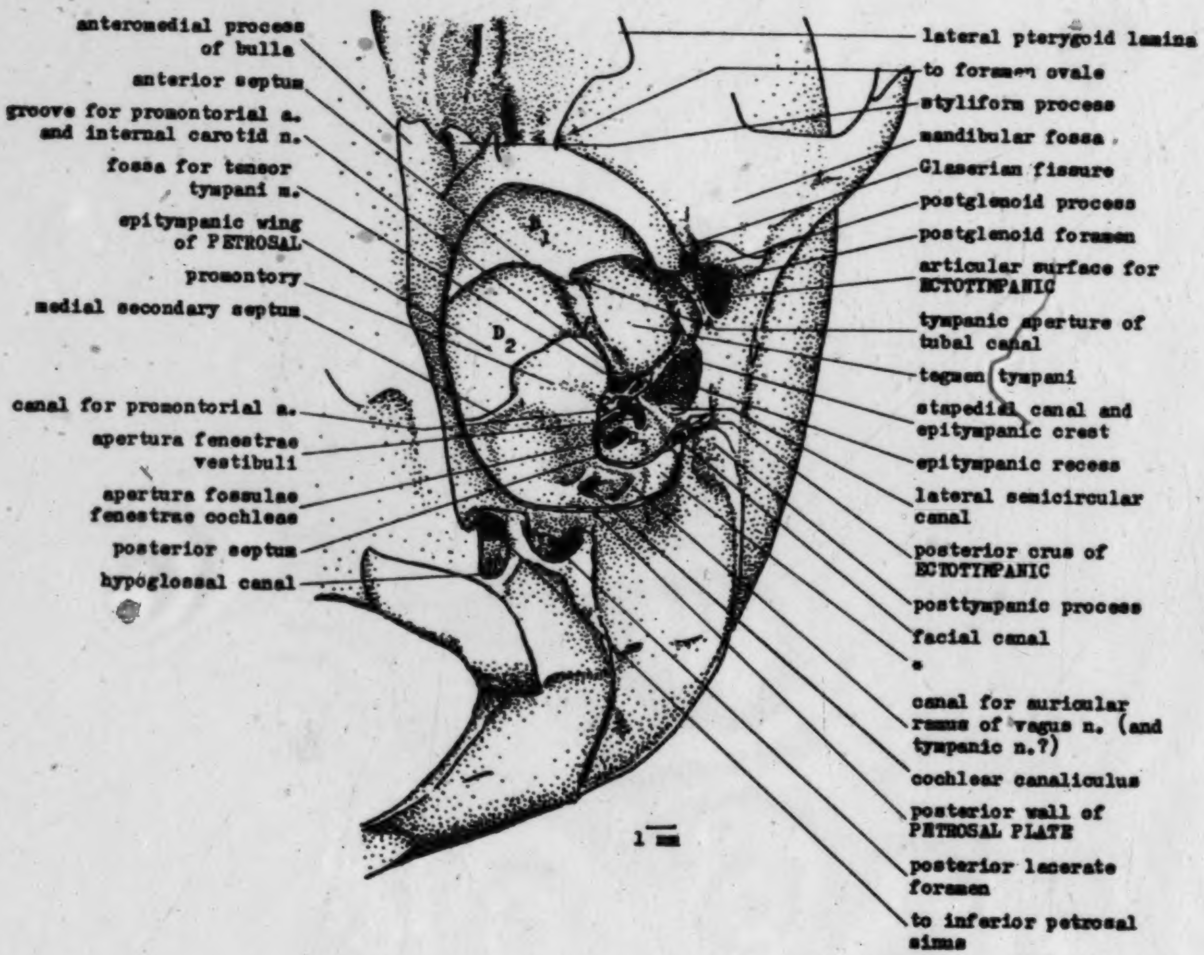

anteromedial process of bulla
anterior septum
groove for promontorial a. and internal carotid n.
fossa for tensor tympani m.
epitympanic wing of PETROSAL
promontory
medial secondary septum
canal for promontorial a.
apertura fenestrae vestibuli
apertura fossulae fenestrae cochleae
posterior septum
hypoglossal canal
lateral pterygoid lamina
to foramen ovale
styliform process
mandibular fossa
Glaserian fissure
postglenoid process
postglenoid foramen
articular surface for ECTOTYMPANIC
tympanic aperture of tubal canal
tegmen tympani
stapedial canal and epitympanic crest
epitympanic recess
lateral semicircular canal
posterior crus of ECTOTYMPANIC
posttympanic process
facial canal
*
canal for auricular ramus of vagus n. (and tympanic n.?)
cochlear canaliculus
posterior wall of PETROSAL PLATE
posterior lacerate foramen
to inferior petrosal sinus
D_1
D_2
1 mm

FIG. II-4 M. murinus MPIH 1964/41 (fetus); s. 865, cross-section, left side; Azan; x 41.

Growth of petrosal plate I. This and the following four figures depict the growth of the anterior part of the petrosal plate (derived from the original rostral tympanic process of the petrosal). In this specimen, the rostral tympanic process is represented by small trabeculae on the ventral surface of the promontory.

The gap between the dorsal part of the promontory and the medial edge of the tegmen tympani is part of the piriform fenestra.

1, greater petrosal n.; 2, promontorial a. and internal carotid n.; 3, tensor tympani m.; 4, chorda tympani; 5, lesser petrosal n.; 6, auricular cartilage; 7, anterior carotid a.

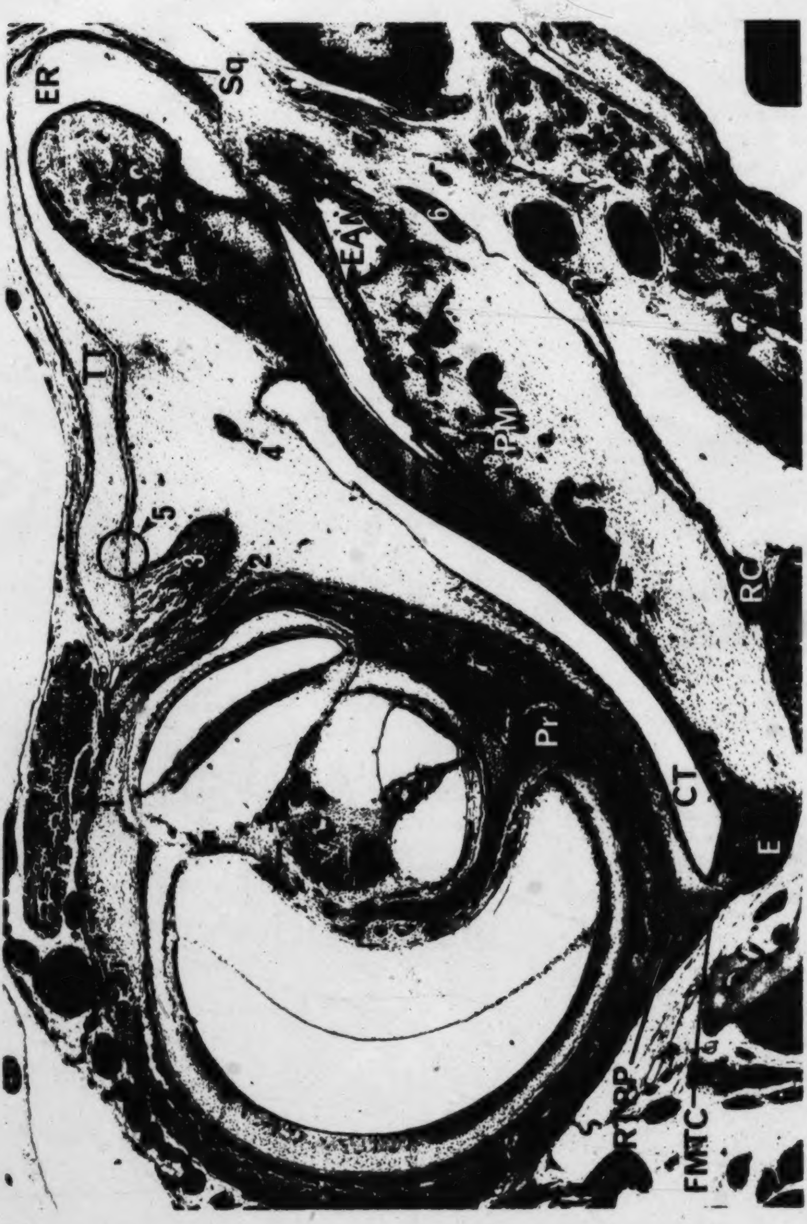

ER
Sq
EAM
6
TT
PM
5
3
2
RC
Pr
CT
E
RtRP
FMTC

FIG. II-5 M. murinus MPIH 1962/57 (fetus); s. 102/1/2, cross-section, left side (sides rev.); Azan; x 38.

Growth of petrosal plate II. The trabeculae composing the rostral tympanic process now form a prominent ridge (see also fig. II-1).

The ridge on the underside of the tegmen tympani is the epitympanic crest. The lesser petrosal n. is within the fossa for the tensor tympani and cannot be easily distinguished in this photograph.

For key to numbered structures, see fig. II-4.

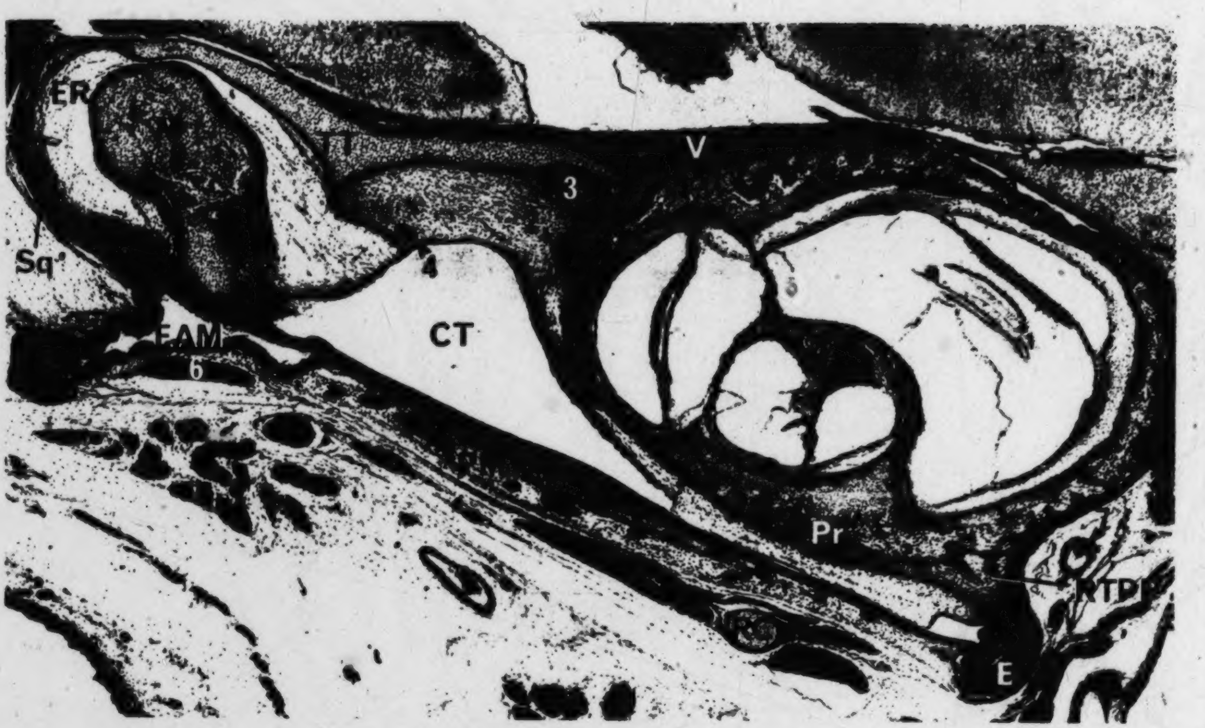

ER
Sq
EAM
6
1
3
V
4
CT
5
Pr
RTP
E

FIG. II-6 M. murinus MPIH 1964/43 (fetus); s. 1124, cross-section, left side; Azan; x 29.

Growth of the petrosal plate III. The petrosal plate is substantially larger, but still occupies the middle of the ventral surface of the promontory.

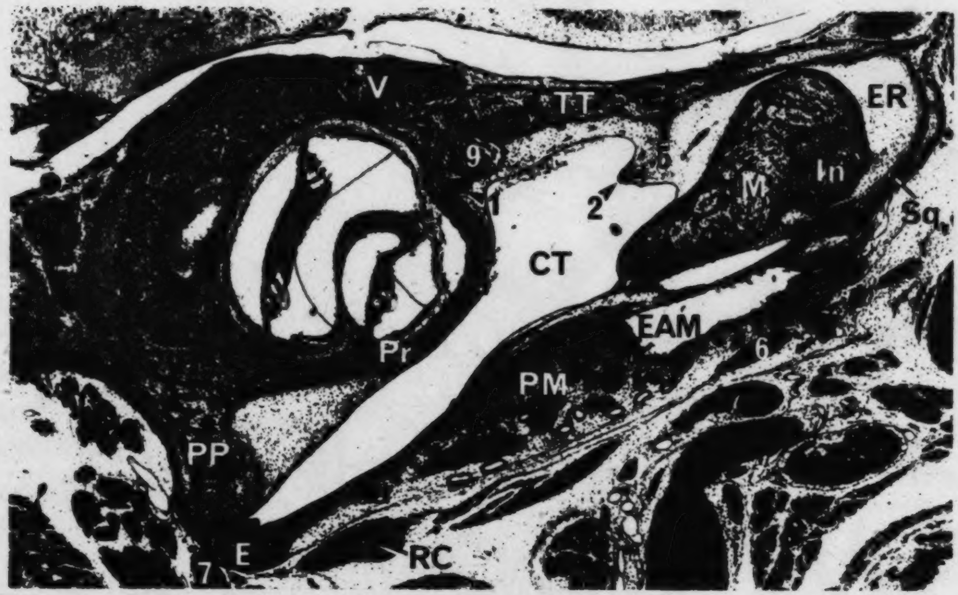
1, promontorial a. and internal carotid n.; 2, chorda tympani; 3, petrosquamous sinus; 4, stapedial a. passing through foramen in tegmen tympani; 5, epitympanic crest; 6, auricular cartilage; 7, anterior carotid a.; 8, cranial cervical ganglion; 9, tensor tympani.

FIG. II-7 M. murinus MPIH 1964/42 (fetus); s. 1120, cross-section, left side; Azan; x 28.

Growth of the petrosal plate IV. The petrosal plate is not significantly larger in this specimen than in the preceding one, but the ventral part of the plate is composed of secondary cartilage.

The stapedial a. is complete in MPIH 1964/42, and anastomizes with the middle meningeal (cf. fig. II-6).

For key to numbered structures, see fig. II-6.


V
TT
ER
9
5
M
In
1
2
Sq
CT
EAM
Pr
6
PM
PP
E
7
RC

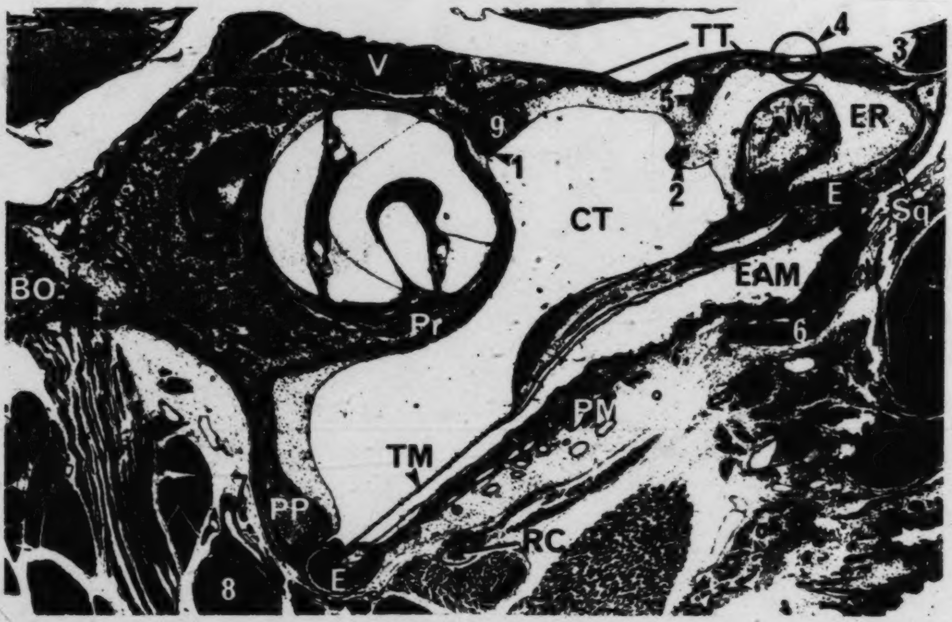

TT
4
3
V
5
M
ER
9
1
2
E
Sq
CT
BO
EAM
Pr
6
PM
TM
PP
7
RC
8
E

FIG. II-8 *L. catta* MPIH 1964/28 (10 days old); s. 2410, cross-section, left side; Azan; x 20.

Growth of petrosal plate V. The petrosal plate is already greatly inflated in this specimen. The plate has grown around the ectotympanic, which is now intrabullar in position. The anterior septum is formed by the everted margins of the tegmen tympani and epitympanic wing of the petrosal, along the persistent remnant of the piriform fenestra.

1, chorda tympani; 2, tunica mucosa; 3, lesser petrosal n.; 4, greater petrosal n.; 5, promontorial a. and internal carotid n.; 6, middle meningeal a. (from stapedial a.); 7, anterior septum.

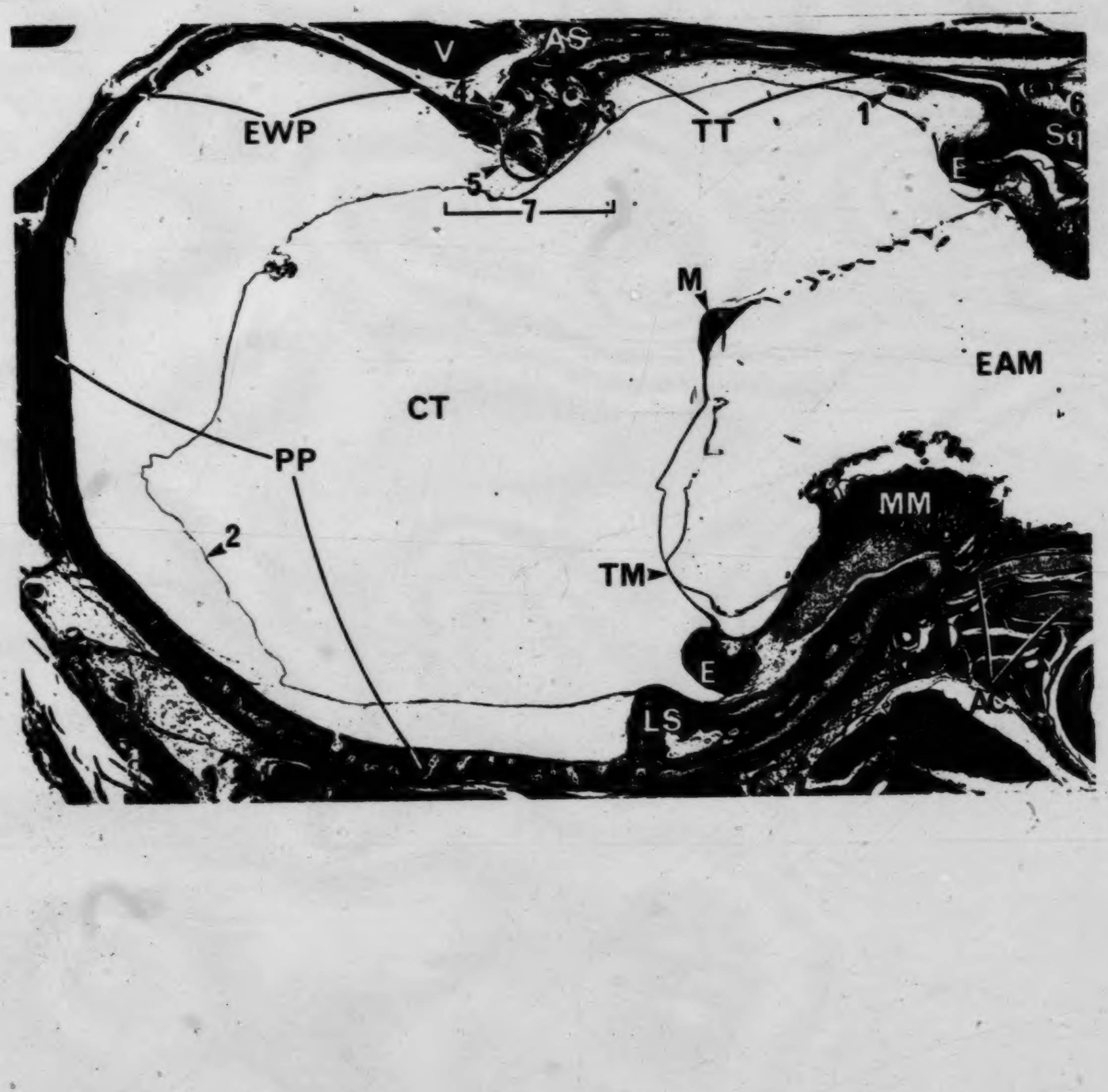

V
AS
EWP
TT
1
6
Sq
E
5
7
M
EAM
CT
PP
2
TM
MM
E
LS
AC

FIG. II-9 *M. murinus* MPIH 1964/41 (fetus); s. 905, cross-section, left side; Azan; x 114.

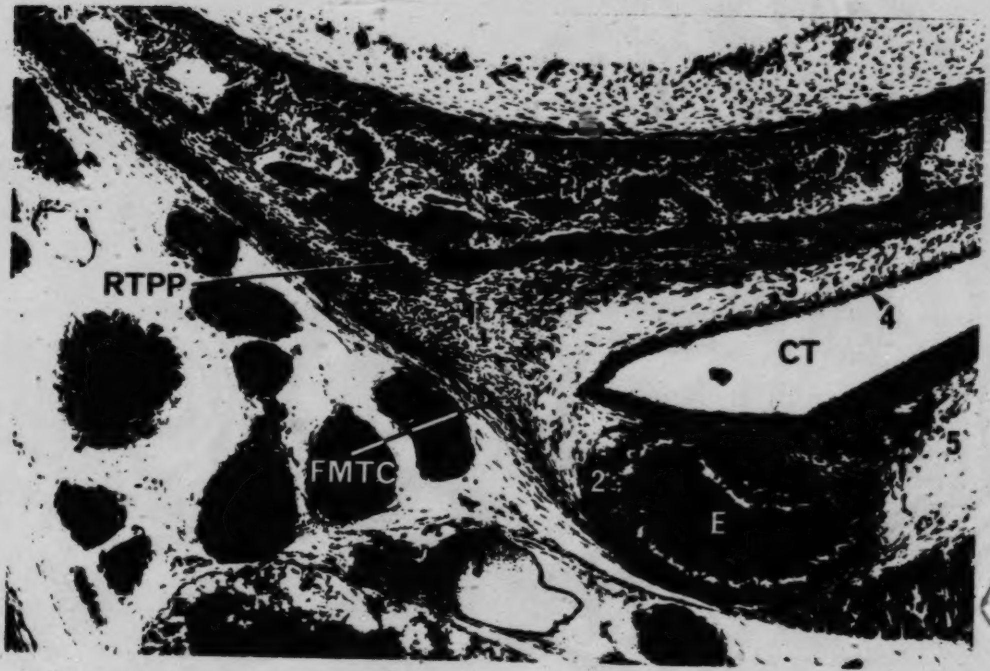
Relationship of ectotympanic and petrosal plate I. In this youngest specimen, the anterior part of the petrosal plate (rostral tympanic process of the petrosal) is a low ridge of trabeculae developing within a periosteal thickening on the promontory. Tympanic mucoid tissue (3) intervenes between the capsular layers of the petrosal plate and ectotympanic (1,2).

1, capsular layer of the petrosal plate; 2, capsular layer of the ectotympanic; 3, tympanic mucoid tissue; 4, epithelium of presumptive tunica mucosa; 5, presumptive tissues of membranous meatus.

FIG. II-10 *M. murinus* MPIH 1962/57 (fetus); s. 102/1/2, cross-section, left side; Azan; x 73.

Relationship of ectotympanic and petrosal plate II. As indicated by the outline arrows, the capsular layers of the petrosal plate and ectotympanic are now contiguous; tympanic mucoid tissue no longer separates them. No separate middle layer is identifiable.

For key to numbered structures, see fig. II-9.


RTPP
1
3
4
CT
FMTC
2
E
5

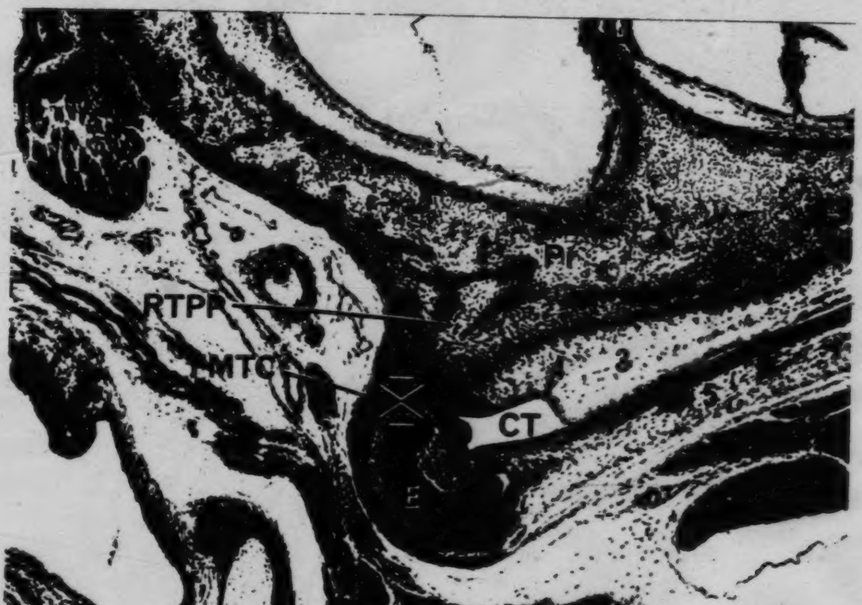

Pr
RTPP
FMTC
3
CT
E
5

FIG. II-11 M. murinus MPIH 1964/43 (fetus); s. 1032, cross-section, right side (sides rev.); Azan; x 120.

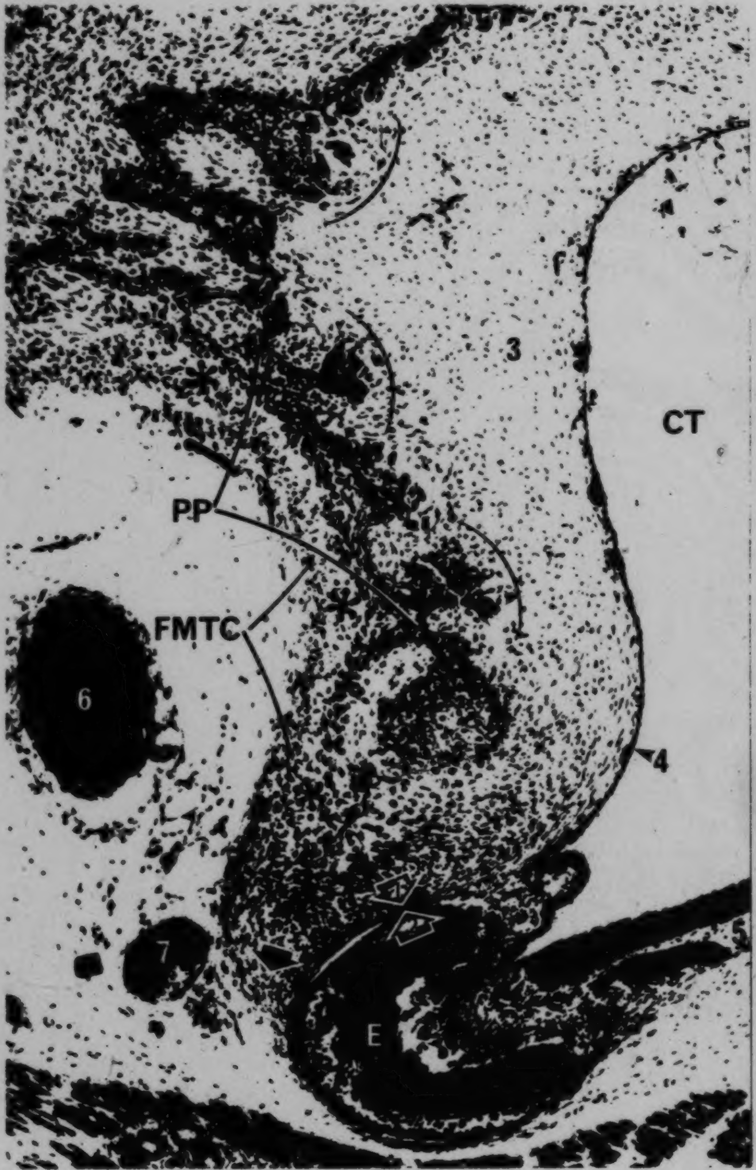
Relationship of ectotympanic and petrosal plate III. No middle layer separates the still-contiguous capsular layers of the ectotympanic and petrosal plate (outline arrows). Osteoblasts (asterisks) densely coat the medial and ventral surfaces of the petrosal plate, while osteoclasts (brackets) can be detected along its lateral surface. Note that the ventromedial edge of the petrosal plate is beginning to grow around the ectotympanic. A lateral uniting layer is seemingly absent.

1, capsular layer of the petrosal plate; 2, capsular layer of the ectotympanic; 3, tympanic mucoid tissue; 4, epithelium of presumptive tunica mucosa; 5, presumptive tissues of membranous meatus; 6, anterior carotid a.; 7, petro-occipital sinus; 8, promontorial a. and internal carotid n.

FIG. II-12 M. murinus MPIH 1964/42 (fetus); s. 1028, cross-section, left side; hematoxylin and eosin; x 84.

Relationship of the ectotympanic and petrosal plate IV. The chief difference between this specimen and MPIH 1964/43 (fig. II-11) is the presence of secondary cartilage in the ventral part of the petrosal plate (black asterisk). A splint of bone of normal appearance (white asterisk) medially bounds the area of secondary cartilage. As before, no middle layer can be distinguished between the contiguous capsular layers.

For key to numbered structures, see fig. II-11.


3
CT
PP
FMTC
6
4
7
E

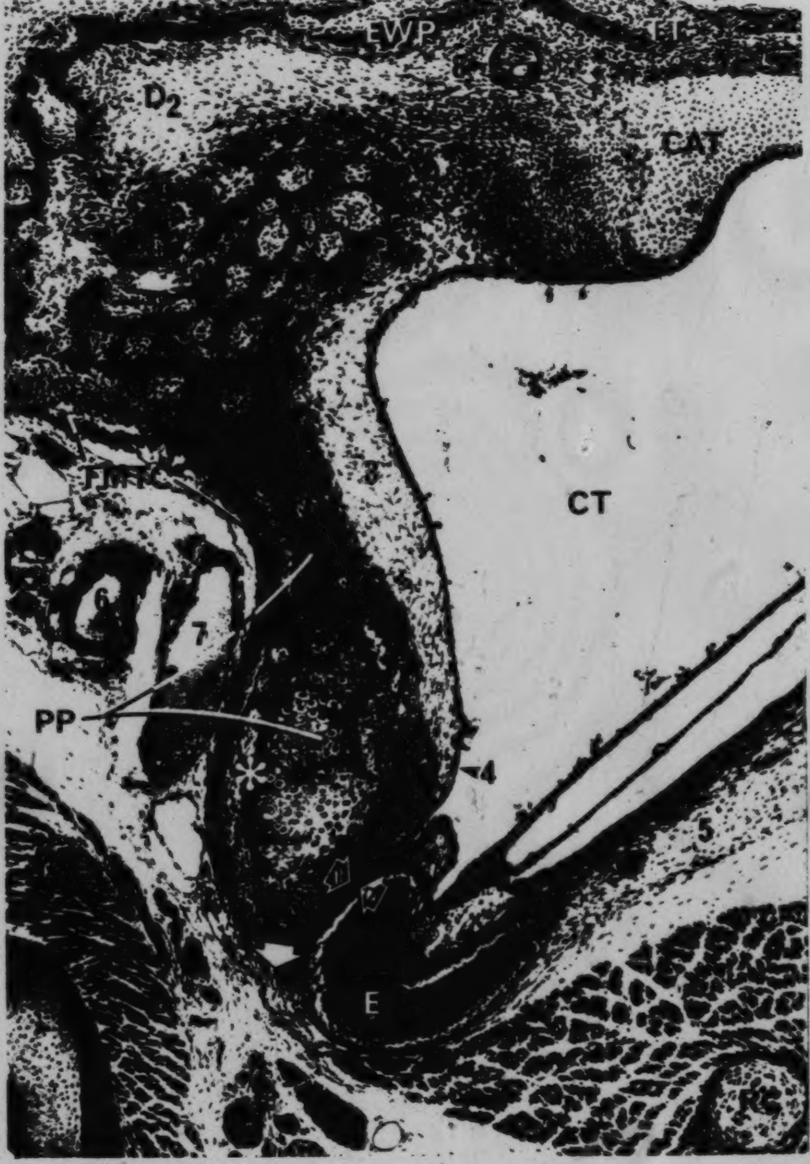

EWP
TT
D₂
CAT
FMTC
3
CT
6
7
PP
4
5
E
RC

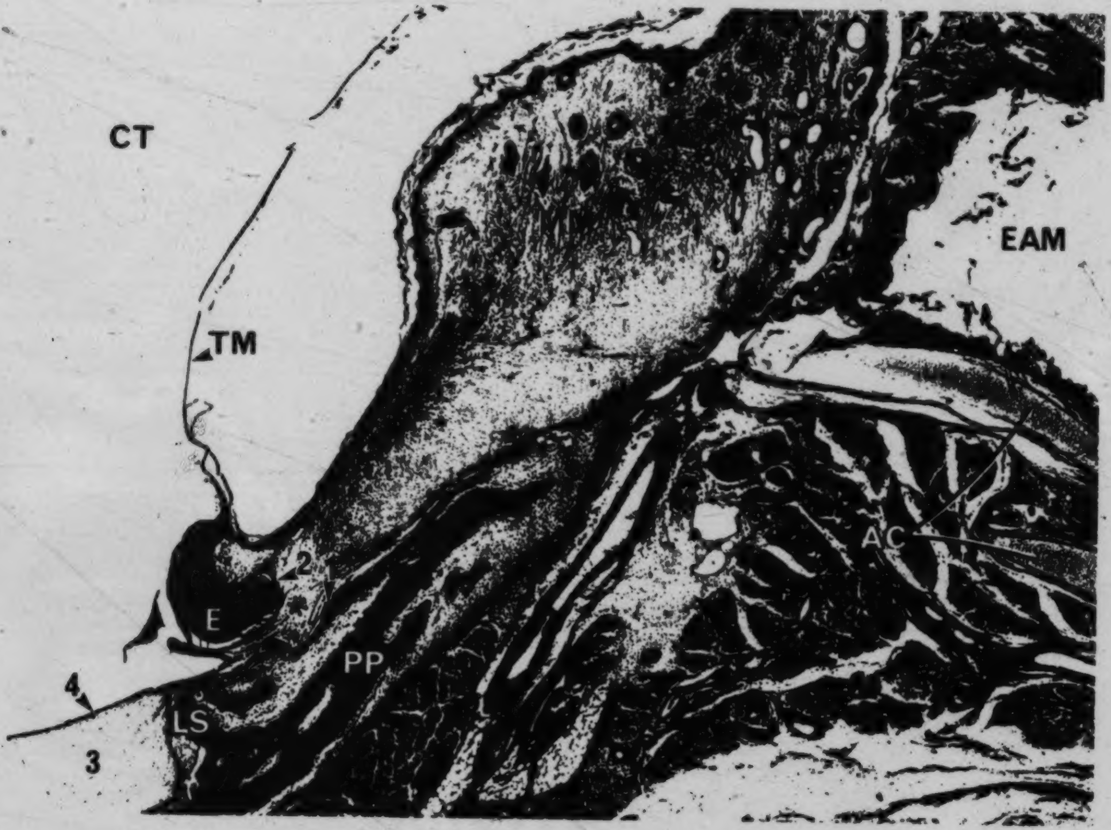
FIG. II-13 L. catta MPIH 1964/28 (10 days old); s. 2320, cross-section, left side; Azan; x 33.

Relationship of ectotympanic and petrosal plate V. The petrosal plate has completely encircled the ectotympanic, and the ectotympanic-petrosal plate relationship has reached its definitive condition. The ectotympanic does not form a suture with the petrosal plate in postnatal life. It remains embedded, as before, within the dermal layer of the membranous meatus, part of which (asterisk) separates the periosteum of the ectotympanic (2) from that of the internal wall of the bulla (1). The fibrous membrane of the tympanic cavity cannot be distinguished from the periosteal tissues lining the external surface of the bulla.

Note the absence of any 'anulus membrane' independent of the tissue forming the membranous meatus, and the extrabullar situation of the auricular cartilage.

For key to numbered structures, see fig. II-11.

FIG. II-14 Schema of sutural layers in a typical suture (after PRITCHARD et al., 1956).


CT
TM
2
E
4
LS
3
PP
EAM
AC

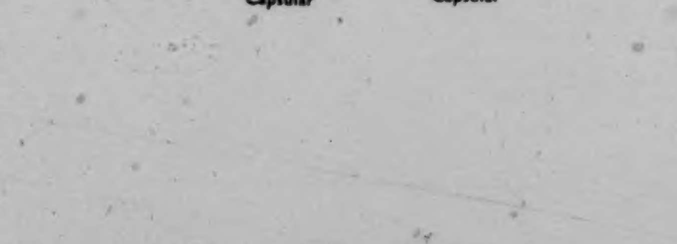

Uniting
Cambial
Capsular
Middle
Capsular
Cambial

FIG. II-15 M. murinus MPIH 1964/41 (fetus); s. 1020, cross-section, left side; Azan; x 28.

Posterior part of presumptive tympanic cavity. The processus recessus is mostly cartilaginous at this stage. Besides defining the ventral limits of the future cochlear canaliculus (accommodating the perilymphatic duct) and the fossula fenestrae cochleae (containing the secondary tympanic membrane), the lateral margin of the processus recessus contributes to the medial part of the caudal tympanic process of the petrosal.

1, tympanic n.; 2, internal carotid a. passing into tympanic cavity; 3, internal carotid n.; 4, stapedius m.; 5, posterior continuation of the crista parotica (serving as lateral section of CTPP); 6, FMTC; 7, medial section of CTPP; 8, vein passing through joint foramen for tympanic n. and auricular ramus of vagus; 9, auricular ramus of vagus; 10, posterior section of CTPP.

FIG. II-16 M. murinus MPIH 1964/41 (fetus); s. 1045, cross-section, left side; Azan; x 43.

The processus recessus per se terminates on the anteroventral margin of the pars canalicularis, but the medial section of the caudal tympanic process of the petrosal continues somewhat further posteriorly (7). The posterior continuation of the crista parotica serves as the lateral section of the caudal tympanic process (5).

For key to numbered structures, see fig. II-15.

FIG. II-17 M. murinus MPIH 1964/41 (fetus); s. 1080, cross-section, right side; Azan; x 52.

The medial section of the caudal tympanic process of the petrosal (7) ends at the joint foramen for the auricular ramus of the vagus n. and the tympanic n. The posterior section of the caudal tympanic process (10) covers the extreme posterior part of the presumptive tympanic cavity, behind the level of this slide. Only its anterior margin is seen here.

For key to numbered structures, see fig. II-15.

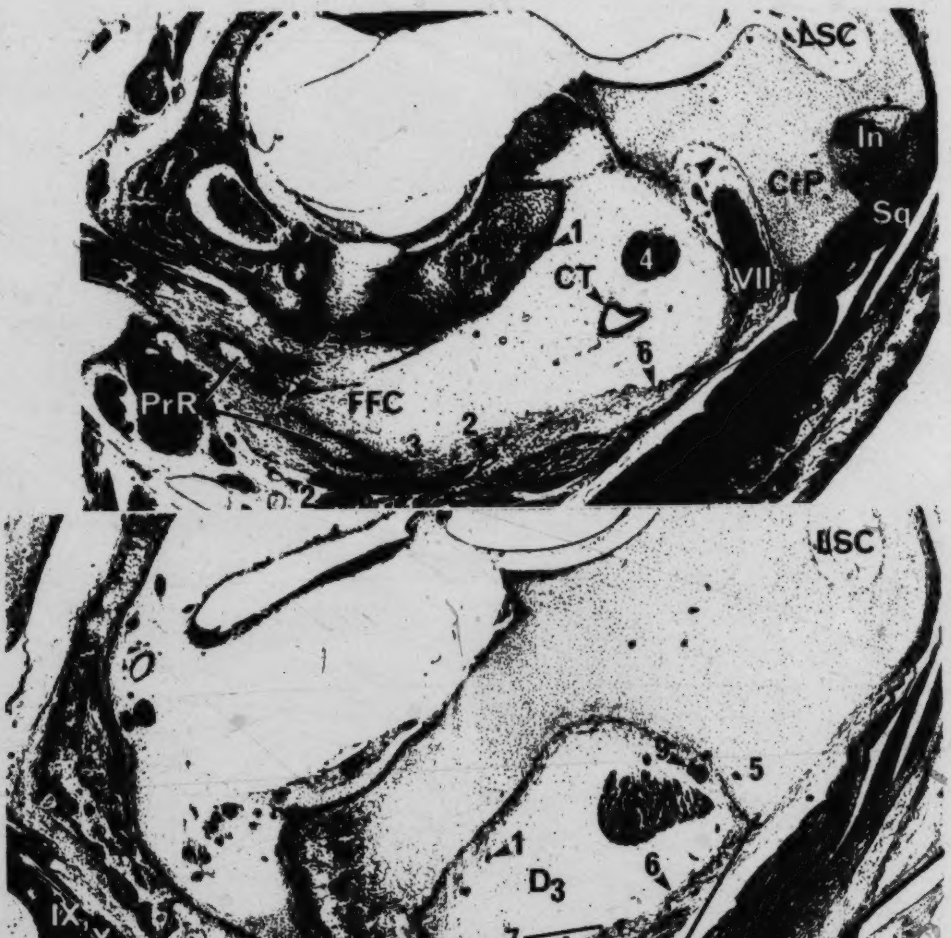

ASC
In
CrP
Sq
1
4
CT
VII
6
PrR
FFC
3
2
2
LSC
5
1
D3
6
7
IX
X
XI
XII
CTPP
LSC
5
9
6
D3
9
8
EO

FIG. II-18 *M. murinus* MPIH 1962/57 (fetus); s. 88/1/1/ cross-section, left side; Azan; x 90.

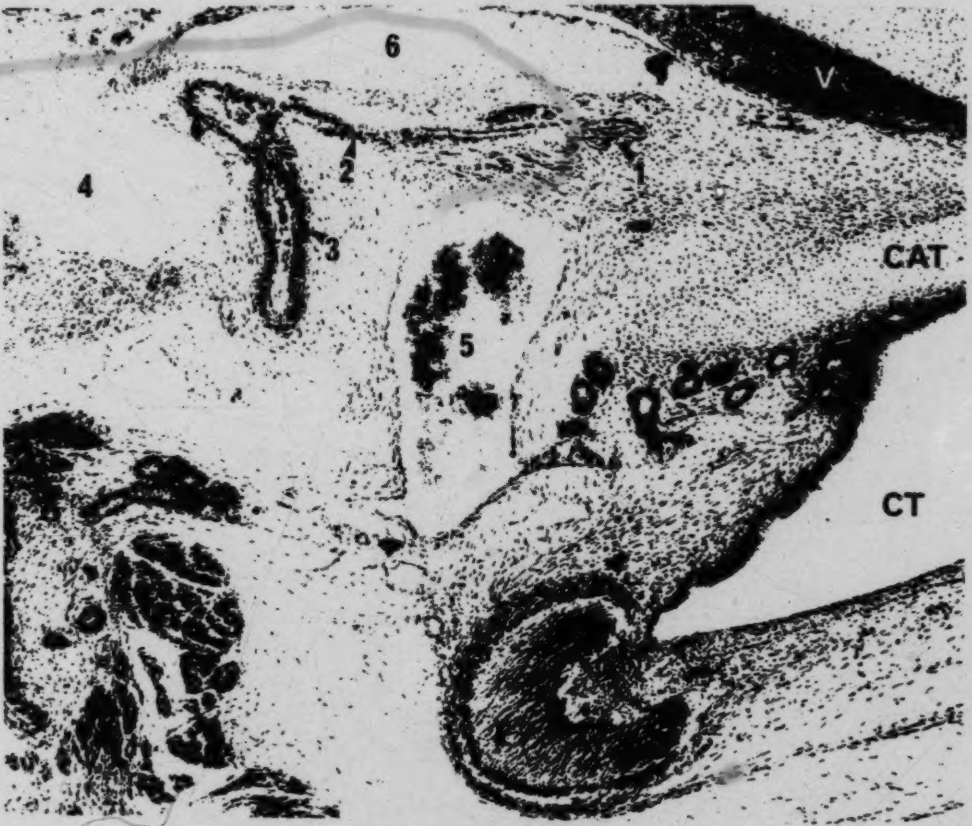
Anastomosis of promontorial and anterior carotid aa.

1, nerves of the pterygoid canal; 2, promontorial a. joining anterior carotid a.; 3, anterior carotid a.; 4, cavernous sinus; 5, petro-occipital sinus; 6, alicochlear commissure.

FIG. II-19 *M. murinus* MPIH 1962/57 (fetus); s. 91/2/3, cross-section, left side; Azan; x 43.

Anterior pole of promontory.

1, promontorial a. and internal carotid n.; 2, anterior carotid a.; 3, petrosquamous sinus in postglenoid foramen; 4, alicochlear commissure; 5, lesser petrosal n.; 6, chorda tympani.


6
V
2
4
3
CAT
5
CT

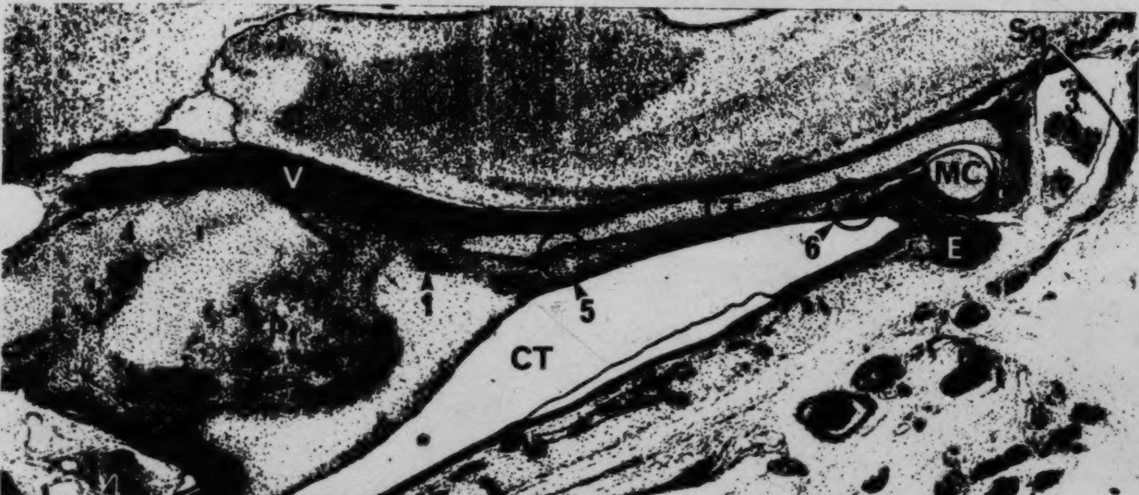

Sa
V
MC
6
E
1
5
CT
2
E

FIG. II-20 M. murinus MPIH 1962/57 (fetus); s. 121/2/3, cross-section, left side; Azan; x 43.

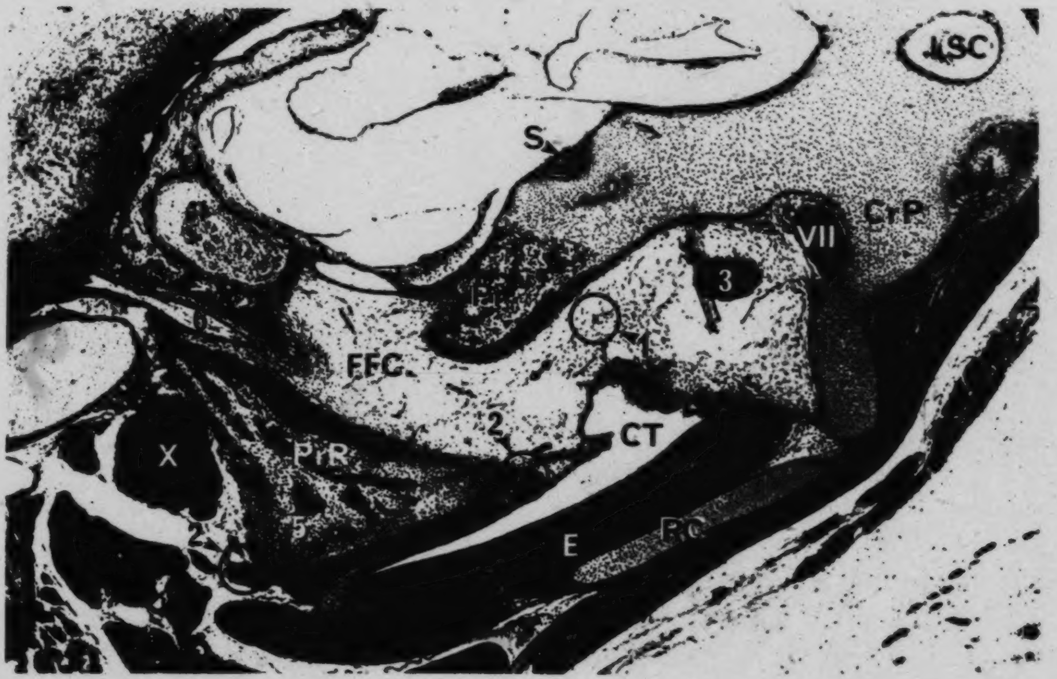
The processus recessus, or medial wall of the apertura fossulae fenestrae cochleae, is bony except for its lateral margin. The trabeculae arising from the ventral surface of the processus are part of the cave-like formation which marks the structural termination of the rostral tympanic process of the petrosal. From this stage onward, the rostral and caudal tympanic processes of the petrosal form a single, continuous rampart, the petrosal plate.

1, tympanic n.; 2, internal carotid a. and n.; 3, stapedius m.; 4, posterior crus of incus; 5, end of RTPP on processus recessus; 6, perilymphatic duct.

FIG. II-21 M. murinus MPIH 1962/57 (fetus); s. 129/1/1, cross-section, left side; Azan; x 43.

Origin of stapedius m. and posterior and lateral sections of caudal tympanic process of petrosal.

1, auricular ramus of vagus entering rear of tympanic cavity; 2, posterior continuation of crista parotica (lateral section of CTPP); 3, stapedius m.; 4, posterior section of CTPP.


LSC
S
CrP
VII
3
1
FFC
2
CT
X
PyR
5
E
PC

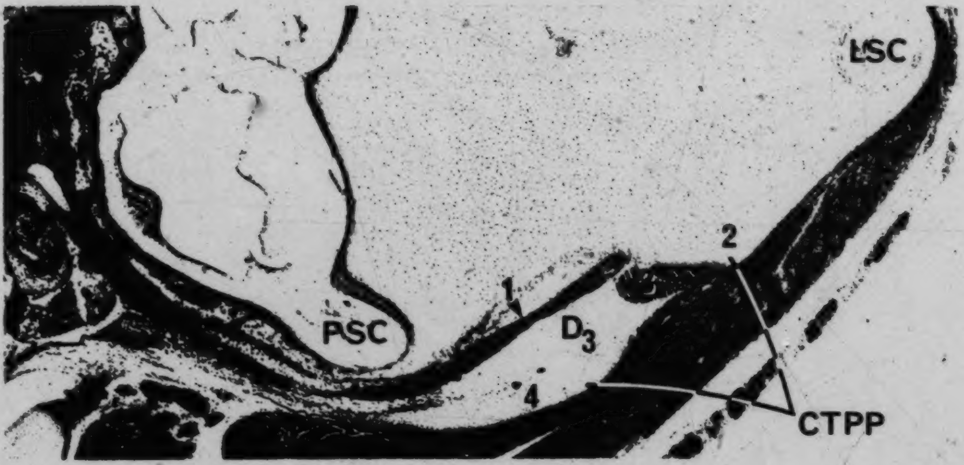

LSC
2
1
PSC
D$_3$
4
CTPP

FIG. II-22 M. murinus MPIH 1964/43 (fetus); s. 1048, cross-section, left side; Azan; x 30.

Anterior part of petrosal plate. Note remnant of piriform fenestra (3).

1, greater petrosal n.; 2, promontorial a. and internal carotid n.; 3, remnant of piriform fenestra; 4, chorda tympani; 5, stylohyal center (in Reichert's cartilage); 6, lesser petrosal n.; 7, anterior carotid a.; 8, alicochlear commissure; 9, auricular cartilage.

FIG. II-23 M. murinus MPIH 1964/43 (fetus); s. 1320, cross-section, right side; Azan; x 31.

Posterior part of petrosal plate. This and the following figure depict the cave-like formation (asterisk) which marks the structural boundary between the original subdivisions of the petrosal plate (rostral and caudal tympanic processes of the petrosal).

1, perilymphatic duct; 2, FMTC; 3, tympanic n.; 4, stapedius m.; 5, internal carotid a. and n.; 6, foramen stylomastoideum primitivum.

FIG. II-24 M. murinus MPIH 1964/43 (fetus); s. 1328, cross-section, right side; Azan; x 31.

See legend of fig. II-23.

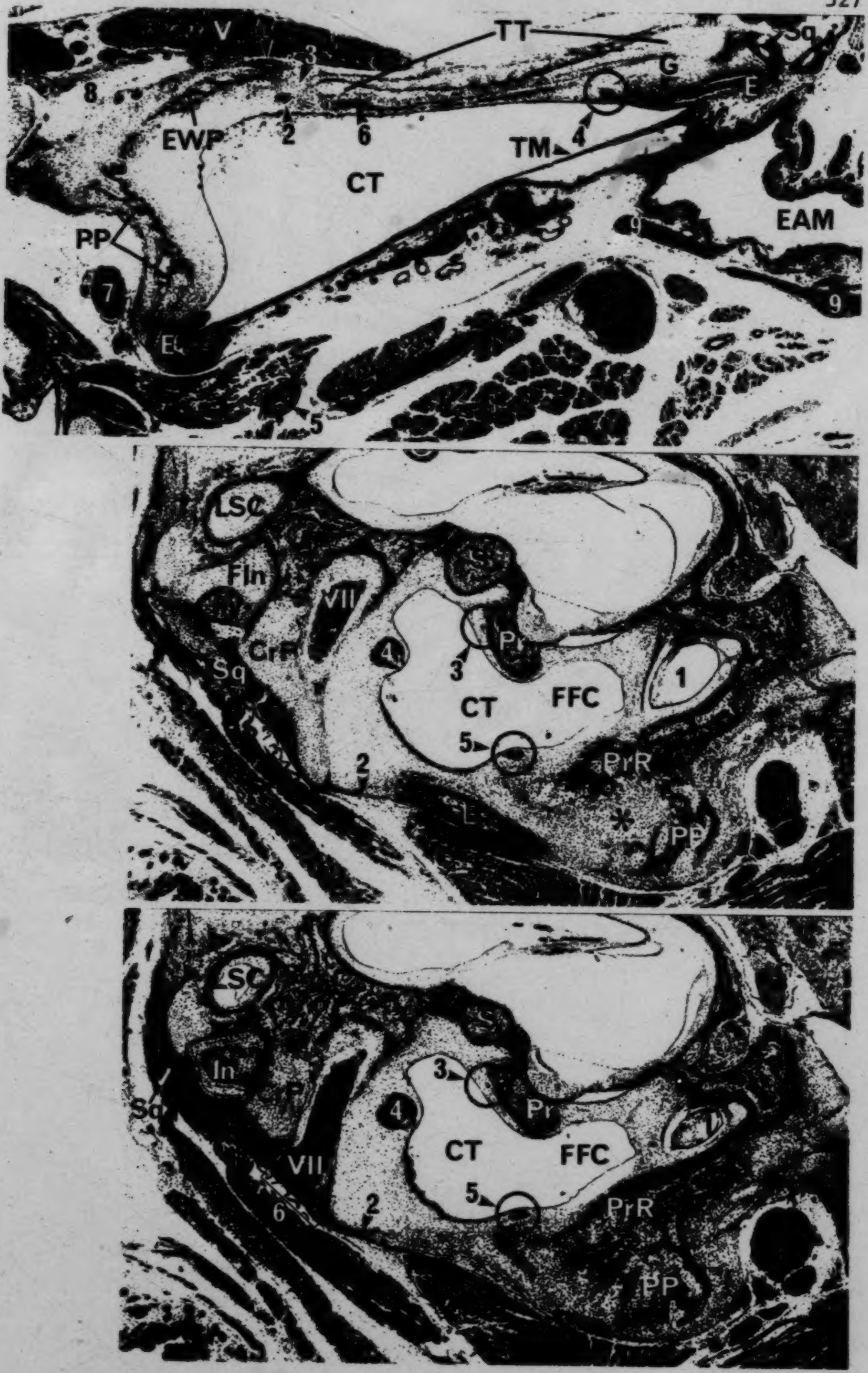

TT
Sq
V
3
G
8
E
EWP
2
6
4
TM
CT
EAM
PP
9
7
9
E
5
LSC
S
Fln
VII
Pr
CrP
4
Sq
3
1
CT
FFC
5
PrR
2
*
PP
LSC
S
In
P
3
Sq
Pr
4
CT
FFC
VII
6
5
PrR
2
PP

FIG. II-25 *M. murinus* MPIH 1964/42 (fetus); s. 1010, cross-section, right side; Azan; x 30.

Anterior end of presumptive tympanic cavity.

1, petro-occipital sinus; 2, anterior carotid a.; 3, alicochlear commissure (degenerating); 4, anteromedial process of bulla; 5, floor of tubal canal (formed by petrosal plate).

FIG. II-26 *M. murinus* MPIH 1964/42 (fetus); s. 1020, cross-section, right side; Azan; x 225.

Secondary cartilage in ventral enlargement of petrosal plate. The arrows indicate the position of the fibrous membrane of the tympanic cavity. The brackets indicate the position of the bone-like tissue on the medial side of the ventral enlargement, while the black asterisk lies in the part of the enlargement which is composed of secondary cartilage. The white asterisks near the top of the figure indicate the position of chondroclast-like cells.

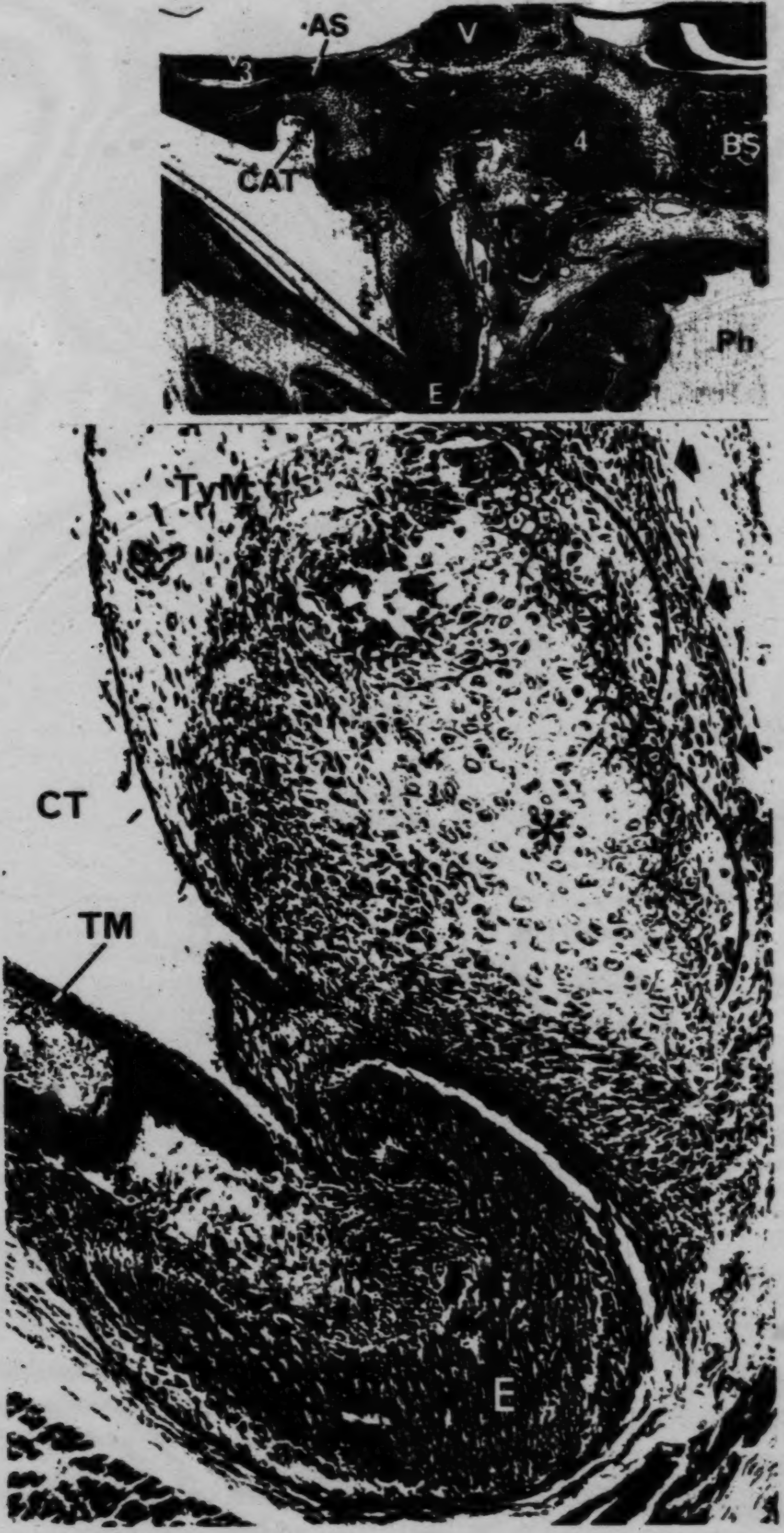

AS
V
V3
CAT
4
BS
Ph
E
TyM
*
CT
TM
E

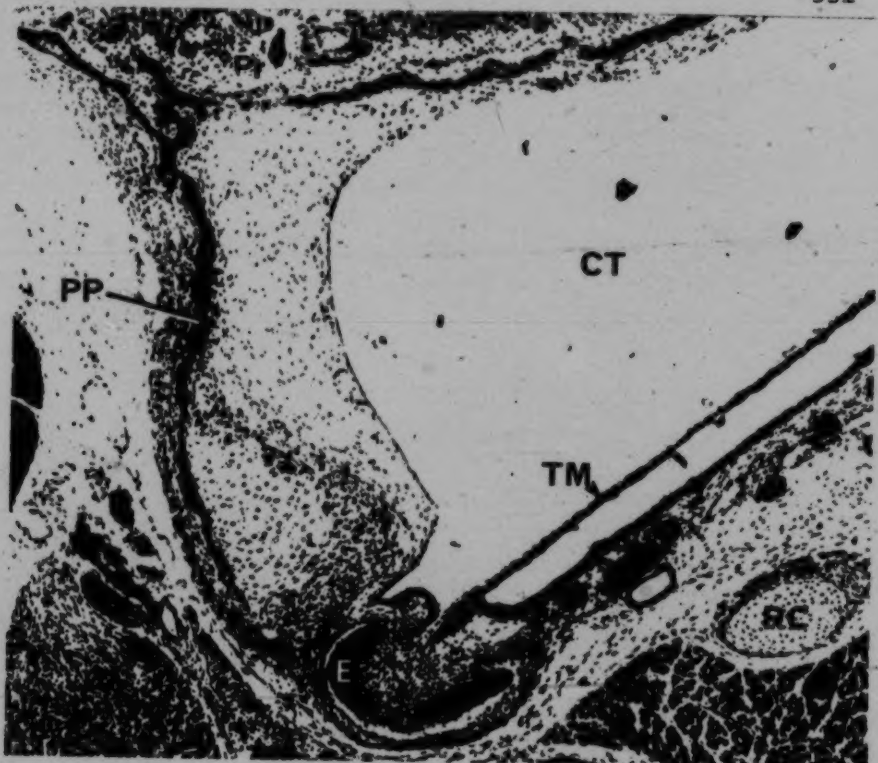
FIG. II-27 M. murinus MPIH 1964/42 (fetus); s. 1126, cross-section, left side; Heidenhain-Woelke; x 85.

With this stain, bone and cartilage cells and bone matrix stain black, while cartilage matrix remains virtually colorless. The secondary cartilage of the petrosal plate is less organized in appearance than the (primary) cartilage of Reichert's cartilage (lower right).

FIG. II-28 M. murinus MPIH 1964/42 (fetus); s. 1282, cross-section, left side; hematoxylin and eosin; x 43.

The petrosal plate now forms a complete floor beneath the posterior part of the tympanic cavity. (Cf. figs. II-20, II-23, and II-24).

1, internal carotid a.; 2, tympanic n. (tympanic canaliculus separate from mastoid canaliculus in this specimen); 3, perilymphatic duct; 4, internal carotid n.; 5, foramen stylomastoideum definitivum.


Pr
PP
CT
TM
E
RC

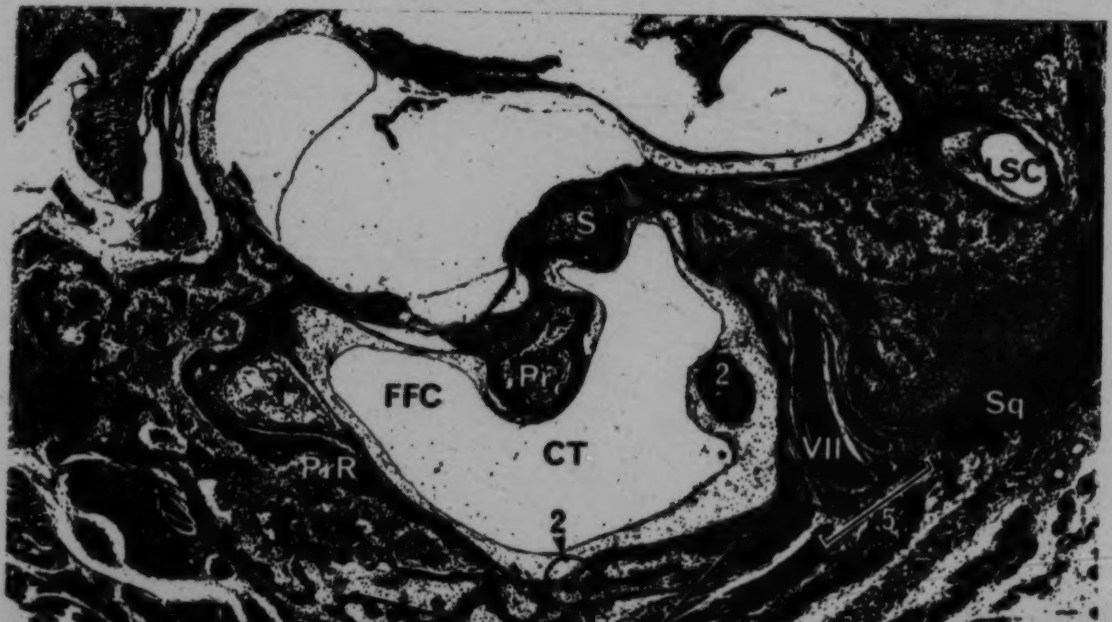

LSC
S
Pr
FFC
2
CT
Pr R
VII
Sq
2
5
1
4
PP

FIG. II-29 M. murinus MPIH 1964/42 (fetus); s. 1240, cross-section, right side; Azan; x 31.

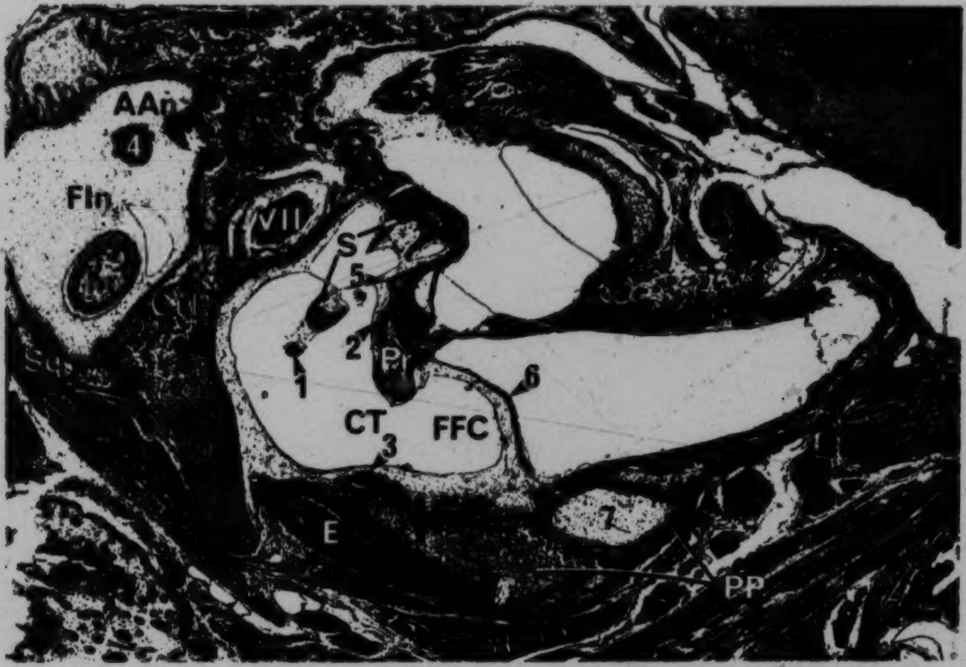
The mastoid cavity is represented by its aditus alone, despite the advanced age of this specimen.

1, tendon of stapedius m.; 2, tympanic n.; 3, internal carotid a. and n.; 4, wall of lateral semicircular canal projecting beneath aditus ad antrum; 5, stapedial a.; 6, secondary tympanic membrane; 7, cave-like formation.

FIG. II-30 M. murinus MPIH 1964/42 (fetus); s. 1320, cross-section, left side; Azan; x 43.

The floor of the posterior part of the tympanic cavity (D_3) is bony, and the origin of the stapedius m. is situated entirely within the cavity itself.

1, ramus auricularis vagi; 2, vein in mastoid canaliculus; 3, posterior continuation of crista parotica (lateral section of CTPP); 4, stapedius m.


AAn
4
FIn
VII
S
5
1
2
Pr
6
CT
3
FFC
E
7
PP

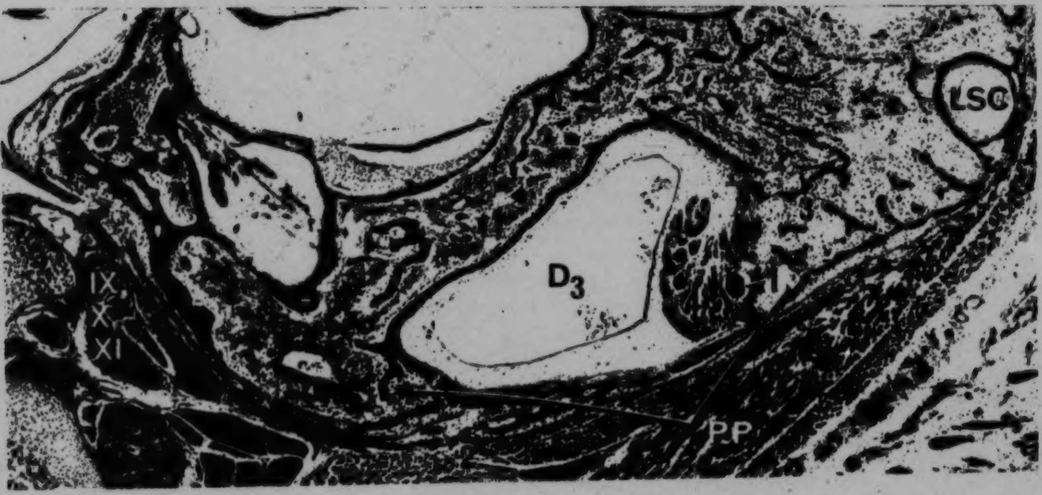

LSC
IX
X
XI
D$_3$
T
PP

FIG. II-31 Propithecus sp. AI 210/211 (fetus); s. 135/2, cross-section, right side; Azan; x 20.

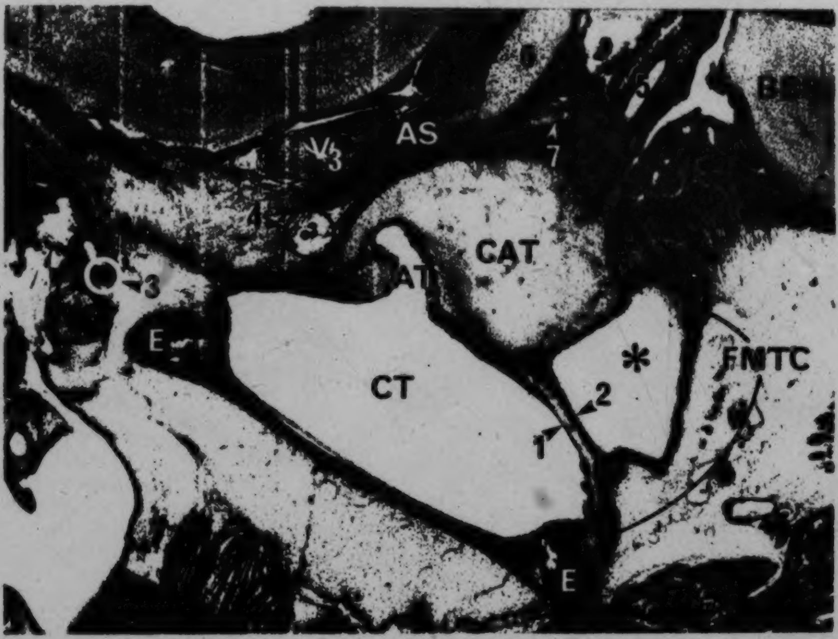
Anterior end of presumptive tympanic cavity. Note the small diverticulum created beneath the cartilage of the auditory tube by the fibrous membrane.

1, epithelium of tunica mucosa (developing); 2, extension of fibrous membrane into tympanic cavity; 3, chorda tympani; 4, lesser petrosal n.; 5, promontorial a. in foramen caroticum primitivum; 6, alicochlear commissure; 7, nerves of the pterygoid canal.

FIG. II-32 Propithecus sp. AI 210/211 (fetus); s. 204/2, cross-section, right side (sides rev.); Azan; x 26.

The cartilaginous caudal tympanic process of the petrosal resembles that of young M. murinus in all essential details except for being somewhat larger (cf. fig. II-21).

1, auricular ramus of the vagus; 2, stapedius m.


B
AS
V3
7
5
BE
4
3
CAT
AT
E
CT
*
FNTC
2
1
E

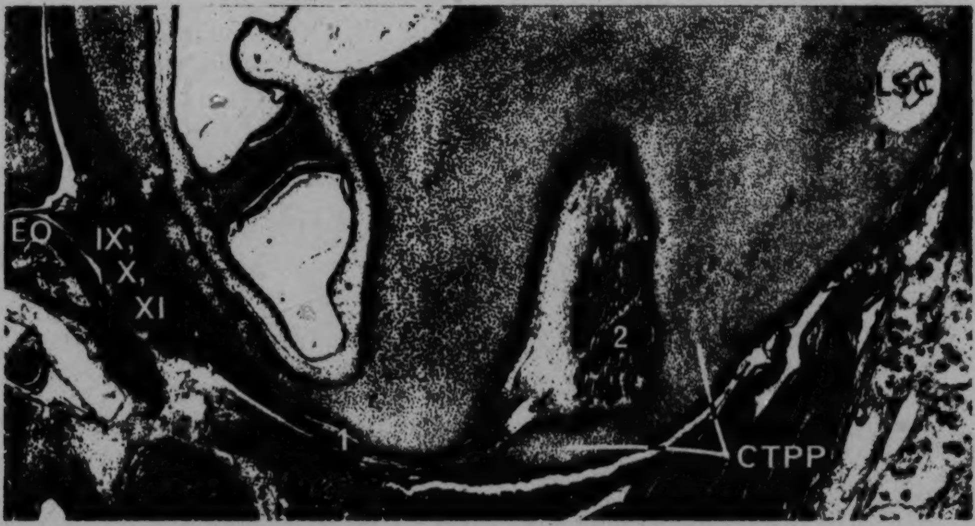

LSC
EO
IX,
X,
XI
2
1
CTPP

FIG. II-33 L. catta MPIH 1964/28 (10 days old); s. 2090, cross-section, right side (sides rev.); Azan; x 19.

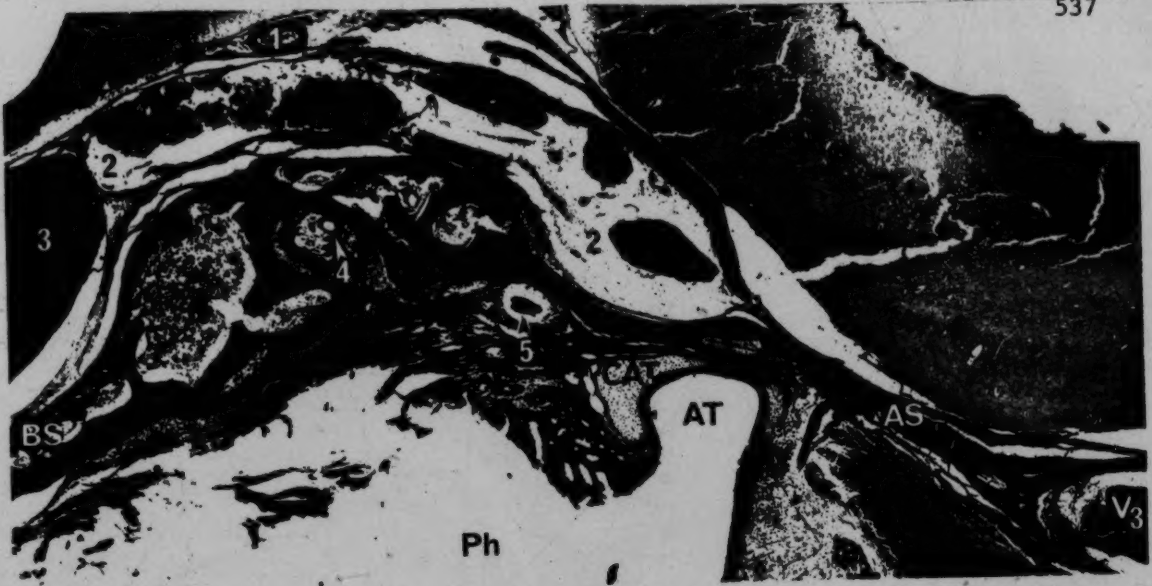
Passage of promontorial a. through anterior carotid canal.

1, circulus arteriosus; 2, cavernous sinus; 3, hypophysis; 4, promontorial a. in true anterior carotid canal; 5, nerves of pterygoid canal.

FIG. II-34 L. catta MPIH 1964/28 (10 days old); s. 2160, cross-section, right side; Azan; x 19.

Anterior wall of bulla, cartilage of the auditory tube, and anteromedial process. The promontorial a. passes between the cartilage of the tube and the anteromedial process in order to reach its canal (see fig. II-33).

1, nerves of pterygoid canal; 2, chorda tympani; 3, promontorial a. (exposed adjacent to anteromedial process of bulla).


1
2
3
2
4
5
BS
AT
AS
V3
Ph

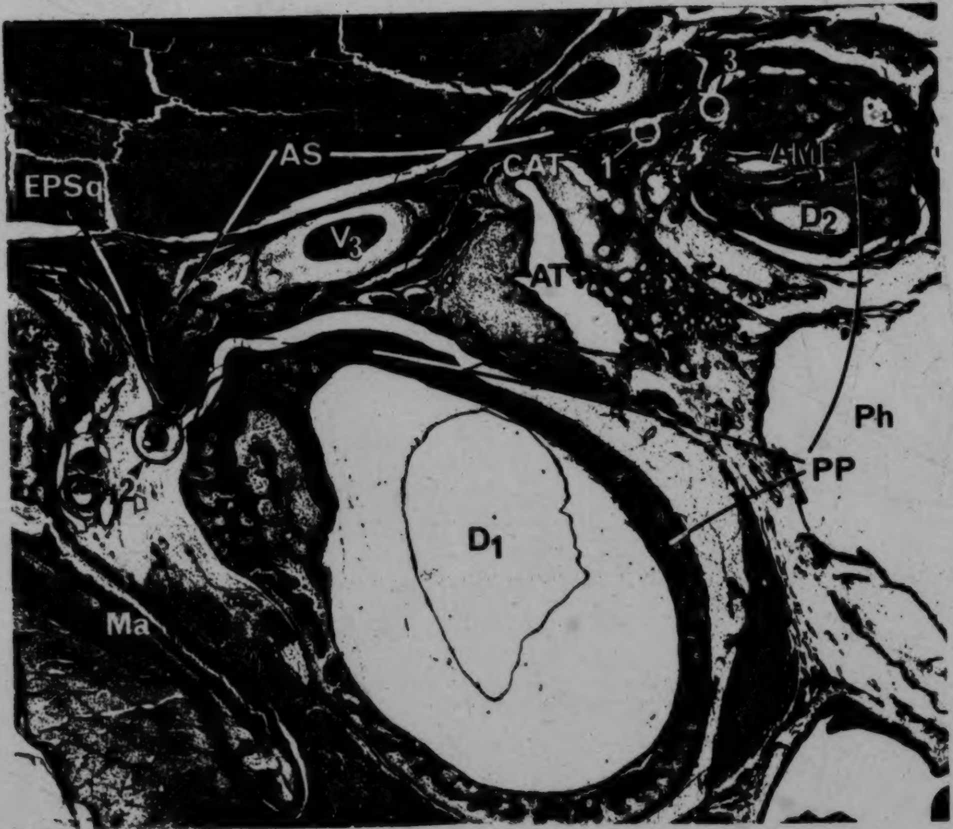

3
AS
CAT
1
AMF
EPSq
D2
V3
AT
Ph
PP
2
D1
Ma

FIG. II-35 L. catta MPIH 1964/28 (10 days old); s. 2550, cross-section, right side; Azan; x 19.

The hypotympanic sinus ends in a posterior diverticulum (part of D_2) which is bounded laterally by the carotid canal and posterior septum. The relations of the posterior septum to this diverticulum indicates that pneumatization splits the original caudal tympanic processes of the petrosal into inner (medial wall of bulla) and outer (posterior septum) tables. See also fig. II-3 for adult conditions.

1, chorda tympani; 2, tensor tympani; 3, internal carotid n.; 4, stapedial a. in its canal; 5, internal carotid a. in its canal; 6, posterior septum; 7, divisions of tympanic n.; 8, greater petrosal n.

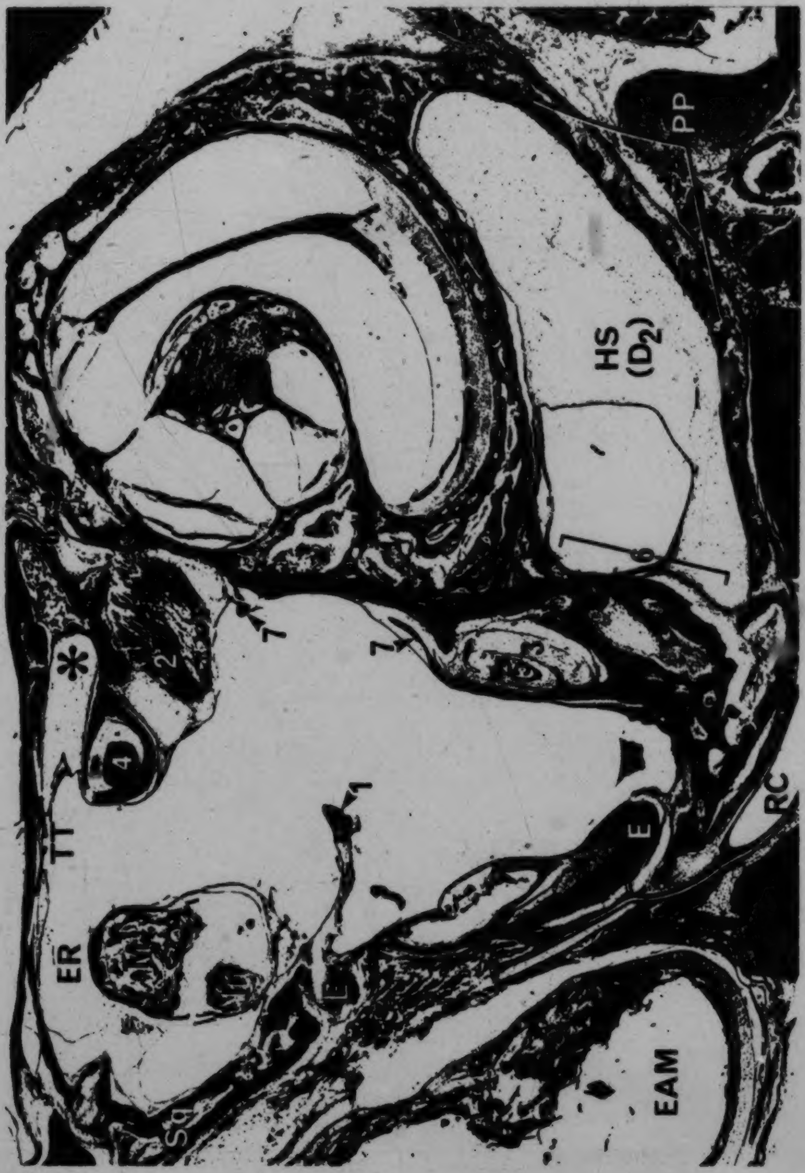

PP
HS
(D$_2$)
*
2
4
TT
ER
M
I
L
Sq
E
RC
EAM

FIG. II-36 *L. catta* MPIH 1964/28 (10 days old); s. 2625, cross-section, right side; Azan; x 19.

Terminal part of posterior diverticulum of hypotympanic sinus (D_2).

1, internal carotid a.; 2, internal carotid n.; 3, secondary tympanic membrane; 4, stapedial a.; 5, posterior septum; 6, chorda tympani in its canaliculus.

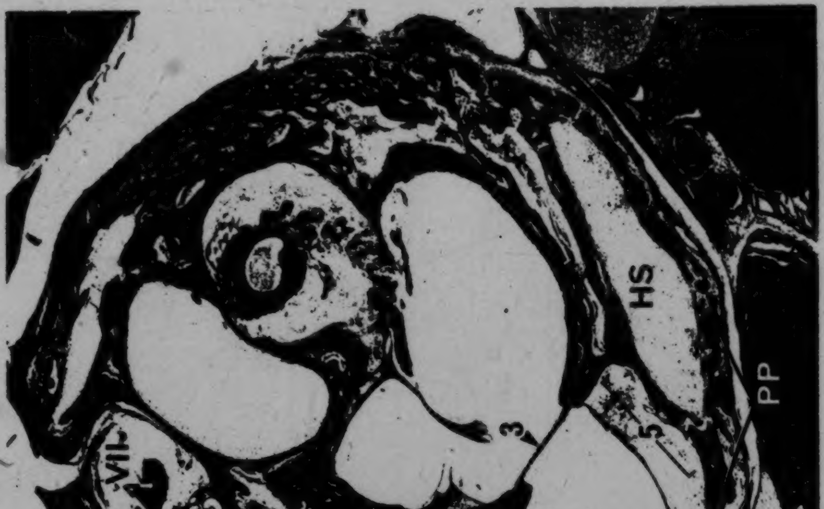

VII
TT
ER
S
CT
3
5
HS
PP
Sq
EAM

FIG. II-37 L. catta MPIH 1964/28 (10 days old); s. 2680, cross-section, right side; Azan; x 19.

Anterior end of mastoid cavity.

1, tendon of stapedius m.; 2, tympanic n. passing through tympanic canaliculus; 3, perilymphatic duct; 4, internal carotid a.

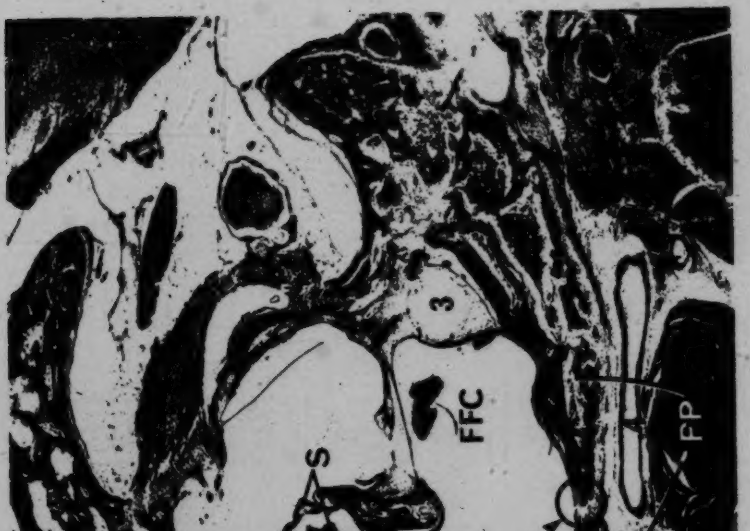

MdC
FIn
VII
CT
FFC
S
1
2
3
FP
EAM

FIG. II-38 L. catta MPIH 1964/28 (10 days old); s. 2735, cross-section, left side; Azan; x 19.

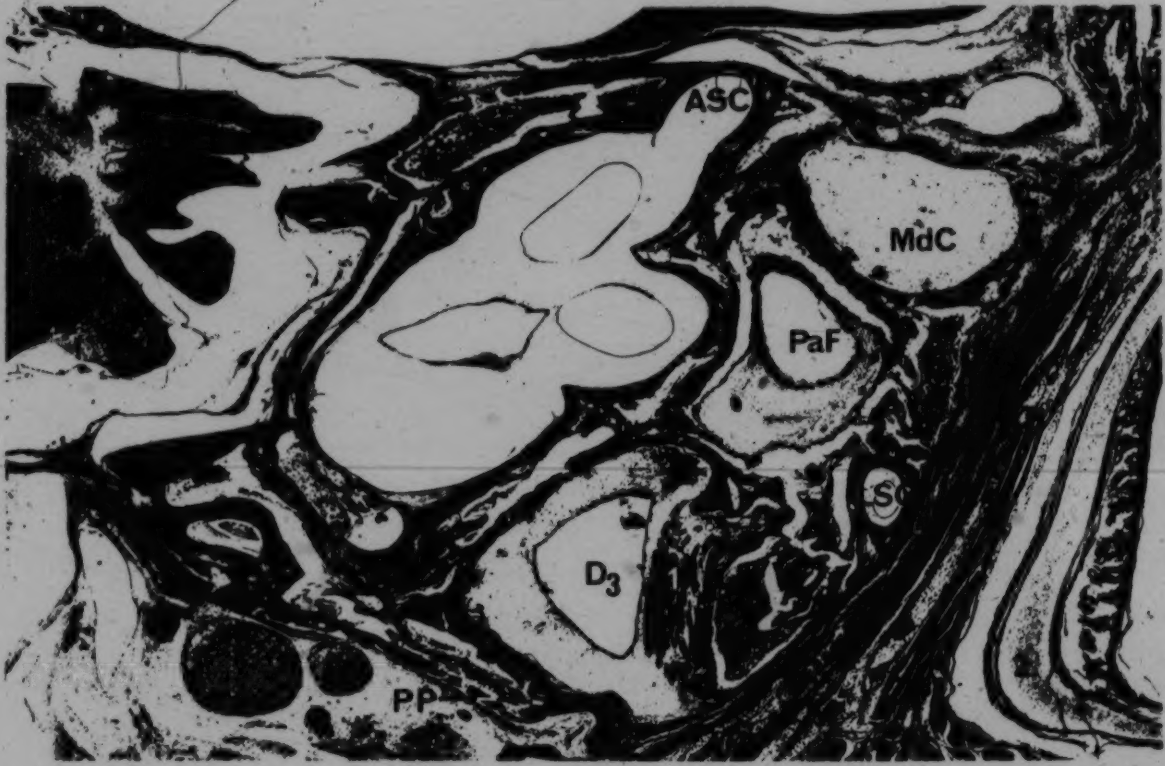
Posterior end of mastoid cavity.

1, stapedius m.; 2, auricular cartilage.

FIG. II-39 L. catta MPIH 1964/28 (10 days old); s. 2550, cross-section, left side; Azan; x 18.5.

Dural branch of stapedial a.

1, dural branch of stapedial a.; 2, tensor tympani m.; 3, greater petrosal n.; 4, stapedial a. (main stem).


ASC
MdC
PaF
SC
D3
PP

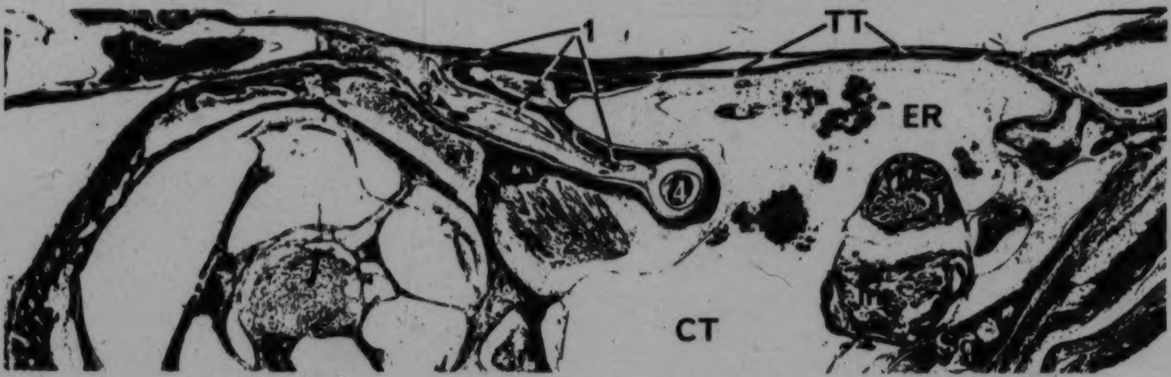

1
TT
ER
4
CT

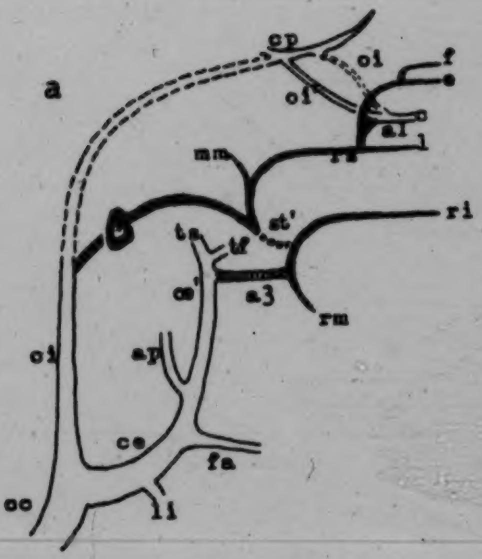
FIG. II-40 Carotid circulation in strepsirhines (diagrammatic); a = *Lemur catta*, b = *Microcebus murinus*, c = *Galago senegalensis*. Diagrams a and c after BUGGE (1974); diagram b is based on the specimens of *M. murinus* used in this study. Method of identification of vessels and anastomoses is that of BUGGE (1974).

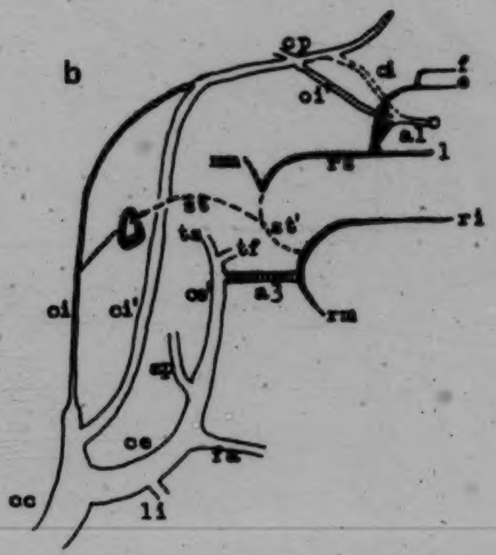
ap - a. auricularis posterior
c - a. ciliaris
cc - a. carotis communis
ce - a. carotis externa (proximal part)
ce' - a. carotis externa (distal part)
ci - a. carotis interna
ci' - apparent internal carotid (anterior carotid)
cp - a. communicans posterior
e - a. ethmoidalis
f - a. frontalis
fa - a. facialis
l - a. lacrimalis
li - a. lingualis
mm - a. meningea media
oi - a. ophthalmica interna
oi' - "internal" ophthalmic a.
ri - ramus infracorbitalis
rm - ramus mandibularis
rs - ramus supraorbitalis
st - a. stapedia
st' - distal part of stapedial artery stem
tf - a. transversa faciei
ts - a. temporalis superficialis

a1 - anastomosis between orbital arteries (l,f,e) from the supraorbital branch (rs) and the ciliary artery (c) from the circulus arteriosus (circle of Willis)

a1' - anastomosis between common stem of frontal (f) and ethmoidal (e) arteries and the circulus arteriosus

a3 - anastomosis between the distal end of the external carotid (ce') and the proximal part of the mandibular branch (rm).


a
cp
oi
f
e
oi'
o
al
l
mm
rs
st'
ri
ts
tf
ce'
a3
rm
ci
ap
ce
fa
cc
li


b
cp
ci
f
e
oi'
o
al
l
mm
rs
st
st'
ri
ts
tf
ce'
a3
rm
ci
ci'
ap
ce
fa
cc
li

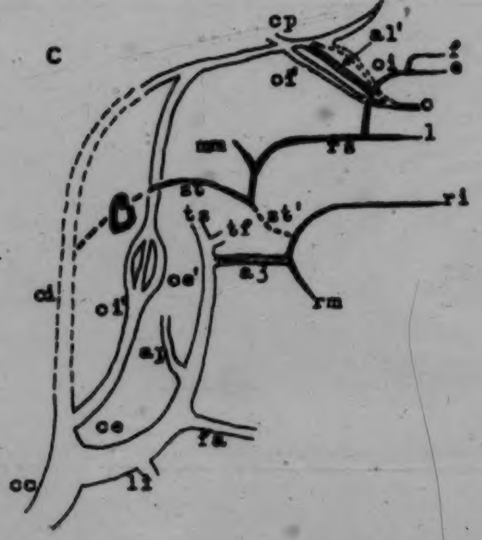

c
cp
al'
oi
f
e
of
o
l
mm
rs
st
ts
tf
st'
ri
ce'
a3
rm
ci
oi'
ap
ce
fa
cc
li

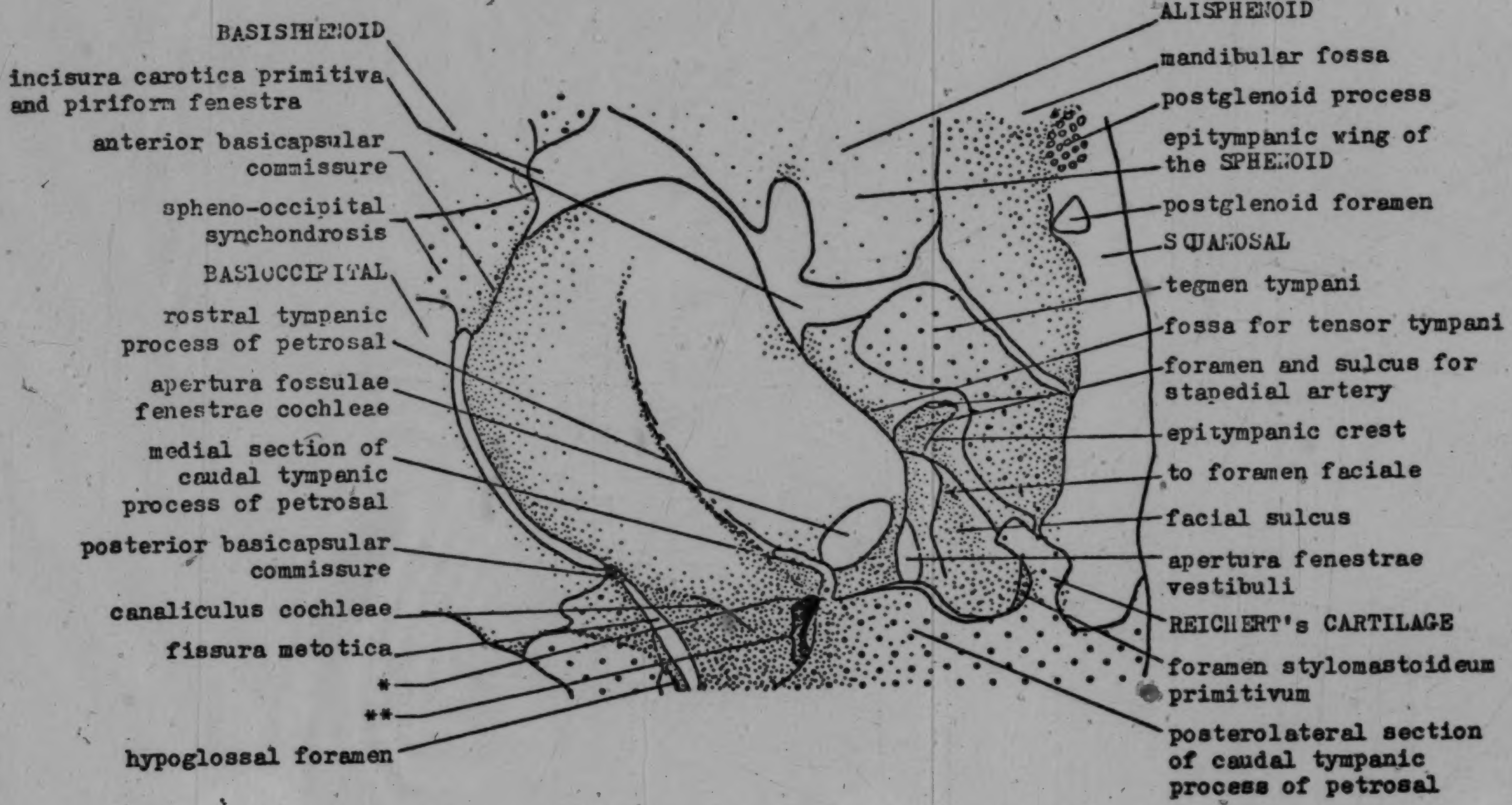
FIG. III-1 G. demidovii MPIH 120 (fetus). Reconstruction of left auditory region and associated structures, ca. x 20. See fig. II-1 for shading conventions.

a. General anatomy.

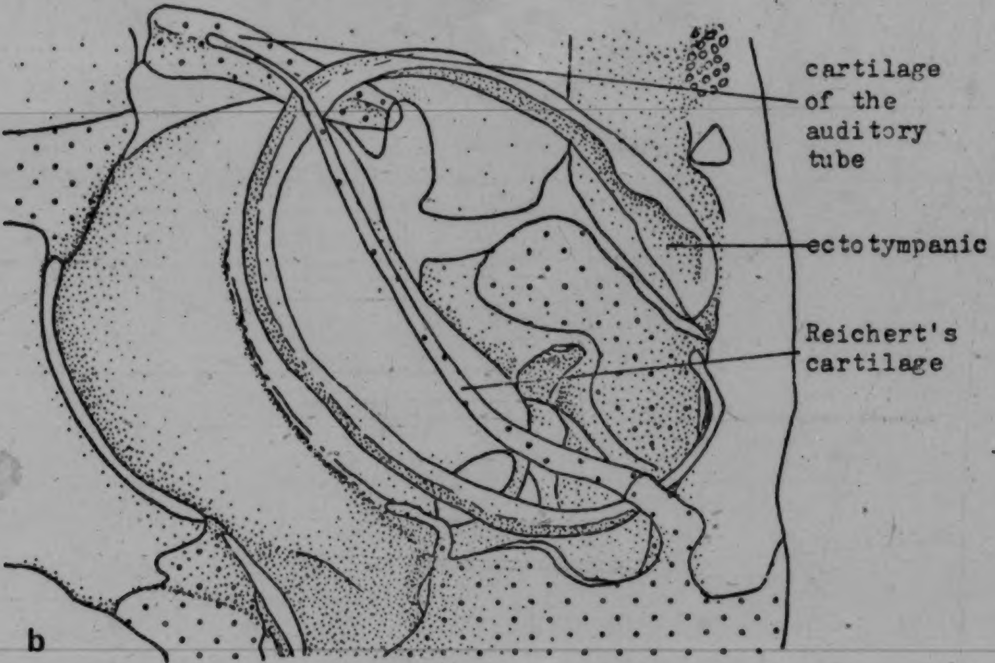
b. Ectotympanic, Reichert's cartilage and cartilage of the auditory tube *in situ*.

c. Routes of arteries and nerves.

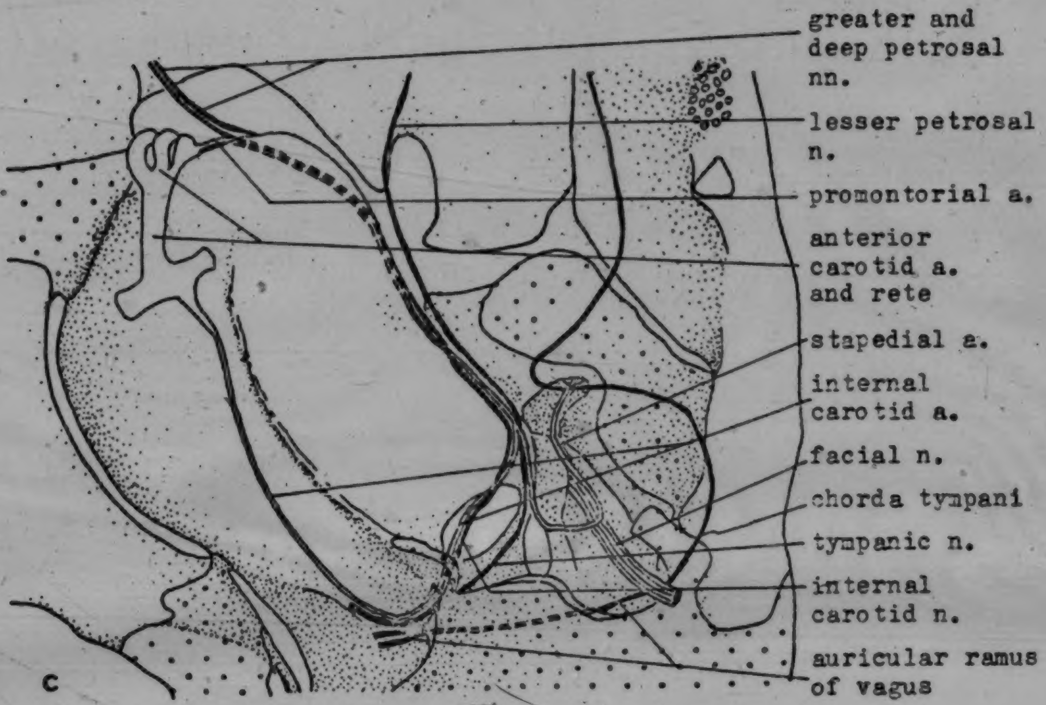
The developing petrosal plate strongly accords with that of fetal M. murinus (fig. II-1) in respect of its origin, positioning and structure. ** - cartilaginous bridge joining medial and posterolateral sections of CTPP; ** - joint foramen in CTPP for internal carotid artery and various nerves.


BASISPHENOID
incisura carotica primitiva and piriform fenestra
anterior basicapsular commissure
spheno-occipital synchondrosis
BASIOCCIPITAL
rostral tympanic process of petrosal
apertura fossulae fenestrae cochleae
medial section of caudal tympanic process of petrosal
posterior basicapsular commissure
canaliculus cochleae
fissura metotica
*
**
hypoglossal foramen
ALISPHENOID
mandibular fossa
postglenoid process
epitympanic wing of the SPHENOID
postglenoid foramen
SQUAMOSAL
tegmen tympani
fossa for tensor tympani
foramen and sulcus for stapedial artery
epitympanic crest
to foramen faciale
facial sulcus
apertura fenestrae vestibuli
REICHERT's CARTILAGE
foramen stylomastoideum primitivum
posterolateral section of caudal tympanic process of petrosal

a


cartilage of the auditory tube
ectotympanic
Reichert's cartilage

b


greater and deep petrosal nn.
lesser petrosal n.
promontorial a.
anterior carotid a. and rete
stapedial a.
internal carotid a.
facial n.
chorda tympani
tympanic n.
internal carotid n.
auricular ramus of vagus

c

FIG. III-2 *G. senegalensis* adult. General view of left auditory region, ventral aspect.

Most of the ventral part of the bulla (petrosal plate and ectotympanic) has been removed in order to expose the cavities of the middle ear. Of particular note is the medial accessory cavity, which is formed by the penetration of the supracochlear and mastoid cavities into the substance of the petrosal plate. The position of diverticulum D_3 is indicated. Since the hypotympanic sinus must be regarded as vestigial or absent, the equivalents of diverticula D_1 and D_2 (of lemurs) are not present in lorises (unless one regards the small fossa on either side of the true anterior septum as such).

*, joint canal for tympani n. and auricular ramus of the vagus,
**, small diverticulum formed within original medial section of the caudal tympanic process of the petrosal.

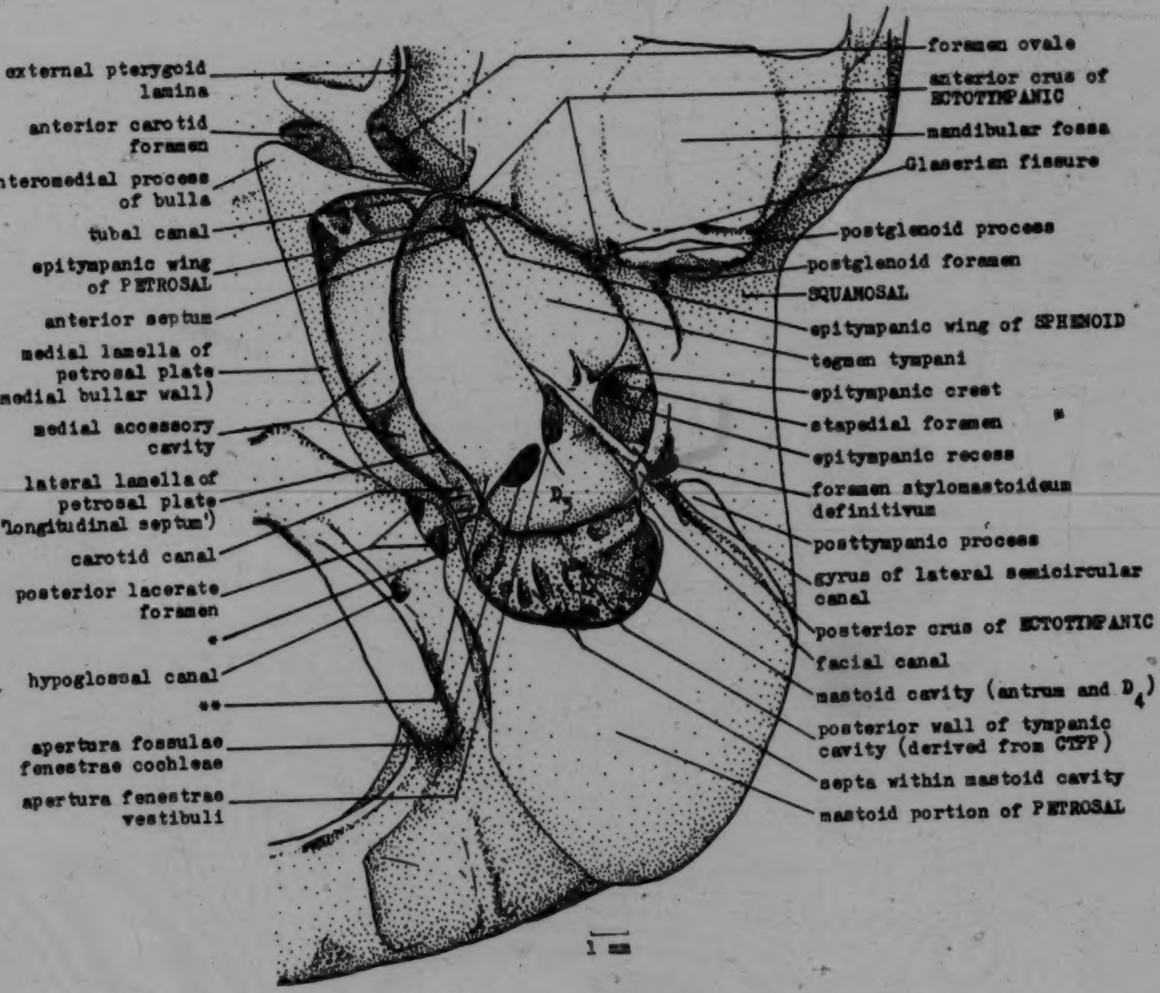

external pterygoid lamina
anterior carotid foramen
anteromedial process of bulla
tubal canal
epitympanic wing of PETROSAL
anterior septum
medial lamella of petrosal plate (medial bullar wall)
medial accessory cavity
lateral lamella of petrosal plate ('longitudinal septum')
carotid canal
posterior lacerate foramen
*
hypoglossal canal
**
apertura fossulae fenestrae cochleae
apertura fenestrae vestibuli
foramen ovale
anterior crus of ECTOTYMPANIC
mandibular fossa
Glaserian fissure
postglenoid process
postglenoid foramen
SQUAMOSAL
epitympanic wing of SPHENOID
tegmen tympani
epitympanic crest
stapedial foramen
epitympanic recess
foramen stylomastoideum definitivum
posttympanic process
gyrus of lateral semicircular canal
posterior crus of ECTOTYMPANIC
facial canal
mastoid cavity (antrum and D_4)
posterior wall of tympanic cavity (derived from CTPP)
septa within mastoid cavity
mastoid portion of PETROSAL
D_3
*
1 mm

FIG. III-3 *G. demidovii* MPIH 125 (fetus); s. 810, cross-section, Kluver-Barrera; x 27.

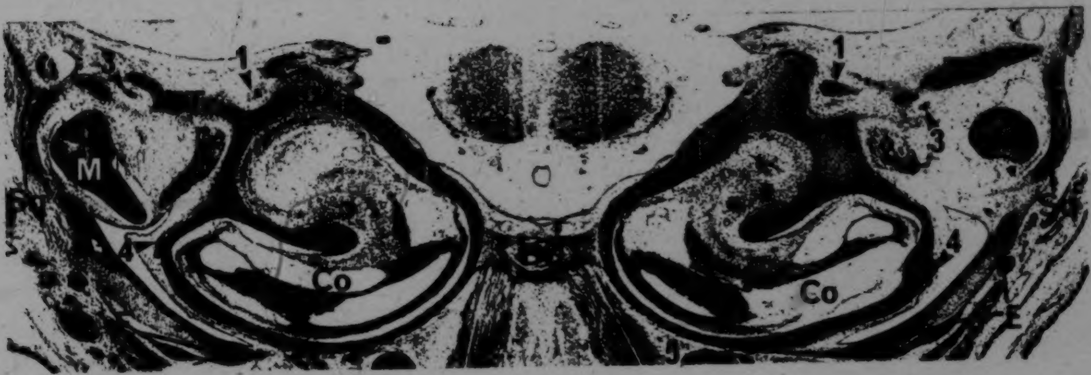
Growth of petrosal plate I. The auditory capsule is completely cartilaginous at this stage. The caudal tympanic process of the petrosal is present in cartilage (see fig. III-12), but the rostral process (which is solely a periosteal outgrowth) does not form until the ventral part of the promontory is ossified.

1, geniculate ganglion in cavum supracochleare; 2, tensor tympani m.; 3, stapedial a.; 4, promontorial a. and internal carotid n.; 5, FMTC.

FIG. III-4 *G. demidovii* MPIH 120 (fetus); s. 1072, cross-section, right side; Cresyl Violet; x 32.

Growth of the petrosal plate II. The pars cochlearis is substantially ossified by this stage and the rostral tympanic process of the petrosal is in the initial phase of its production. The short trabeculae composing the rostral process form a nearly-complete rampart of bone on the ventral surface of the promontory (see fig. III-1). Posteriorly, the rostral process adjoins the partly ossified caudal tympanic process of the petrosal (see figs. III-14, III-15).

1, anterior carotid a.; 2, chorda tympani; 3, lesser petrosal n.; 4, promontorial a.; 5, tensor tympani m.; 6, tympanic plexus in remnant of piriform fenestra; 7, auricular cartilage.


1
1
M
3
4
4
Co
Co
E

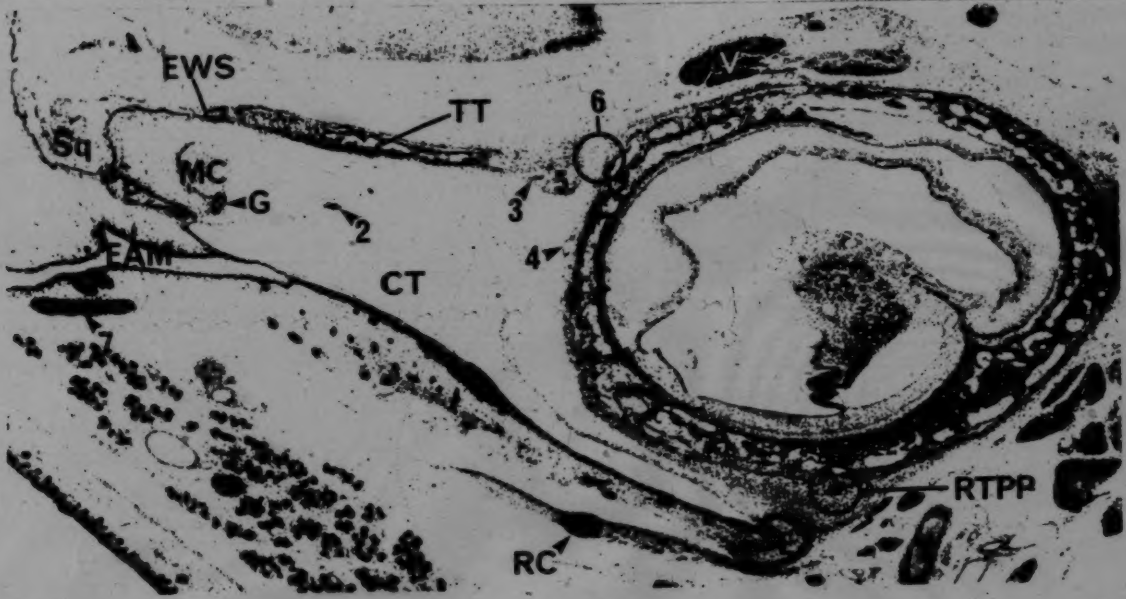

EWS
V
TT
6
Sq
MC
G
2
3
5
EAM
4
CT
7
RTPP
RC

FIG. III-5 *G. senegalensis* MPIH 1962/40 (newborn); s. 178/1, cross-section, left side; Azan; x 19.

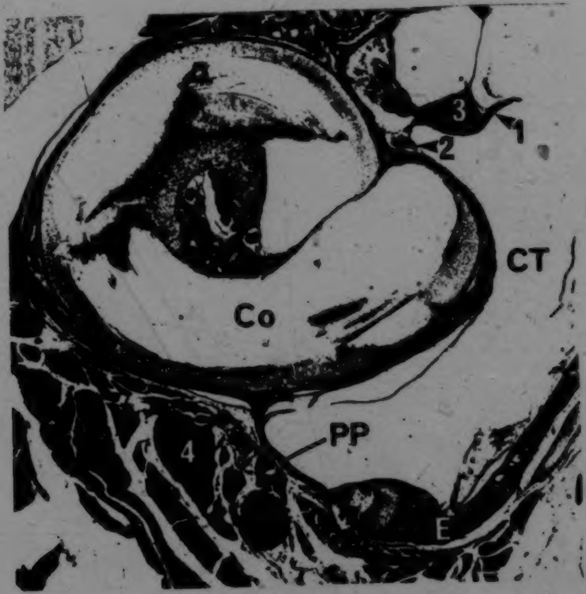
Growth of petrosal plate III. The petrosal plate is now quite large and bears a prominent ventral enlargement (as in young *M. murinus*; cf. figs. II-6, II-7).

1, chorda tympani travelling around tensor tympani m.; 2, internal carotid n.; 3, tensor tympani m.; 4, cranial cervical ganglion of autonomic nervous system.

FIG. III-6 *G. senegalensis* MPIH 1967/117 (10 days old); s. 530, sagittal, left side; Azan; x 15.

Growth of petrosal plate IV. The petrosal plate has begun to fuse with the ectotympanic (see also fig. III-9), thus producing the compound bulla characteristic of lorises. The final phase of bullar maturation involves the pneumatization of the entire petrosal plate and its division into medial and lateral lamellae (see figs. III-26, III-28). The mastoid cavity also extensively inflates the bone surrounding the parafloccular fossa.

1, chorda tympani; 2, stapedial a.; 3, tensor tympani m.; 4, auricular ramus of vagus; 5, internal carotid a. on tip of septum; 6, paraflocculus.


3
1
2
CT
Co
PP
4
E

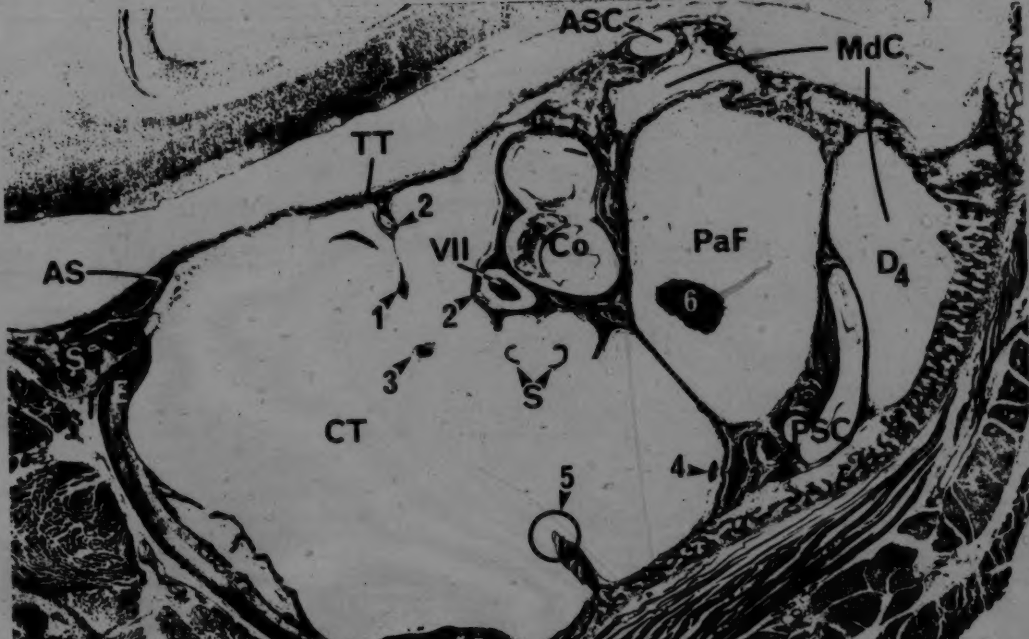

ASC
MdC
TT
2
AS
VII
Co
PaF
D$_4$
1
2
6
S
S
3
CT
E
PSC
4
5
E
PL
RC

FIG. III-7. G. demidovii MPIH 120 (near-term fetus); s. 1198, cross-section, right side; Cresyl Violet; x 116.

Relationship of ectotympanic and petrosal plate I. Cresyl Violet does not adequately stain connective tissue fibres, and boundaries between sutural layers cannot be distinguished with certainty. The denser-staining area on the right is probably the fibrous membrane of the tympanic cavity.

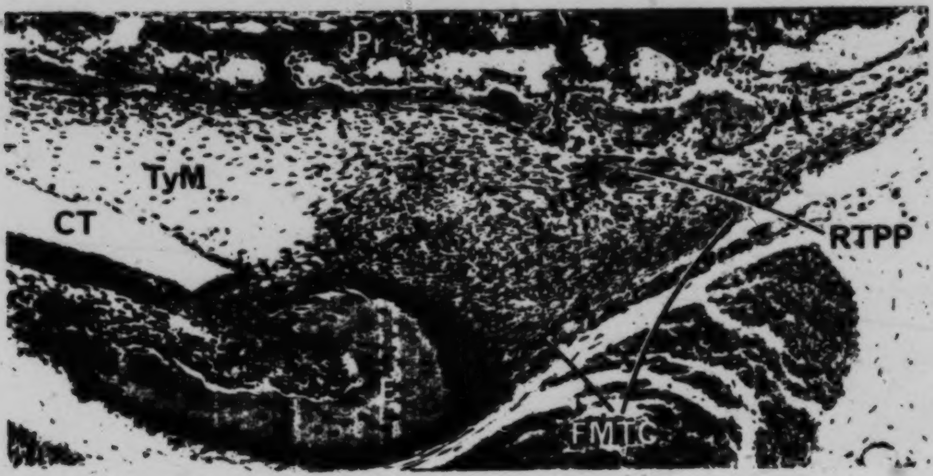
FIG. III-8

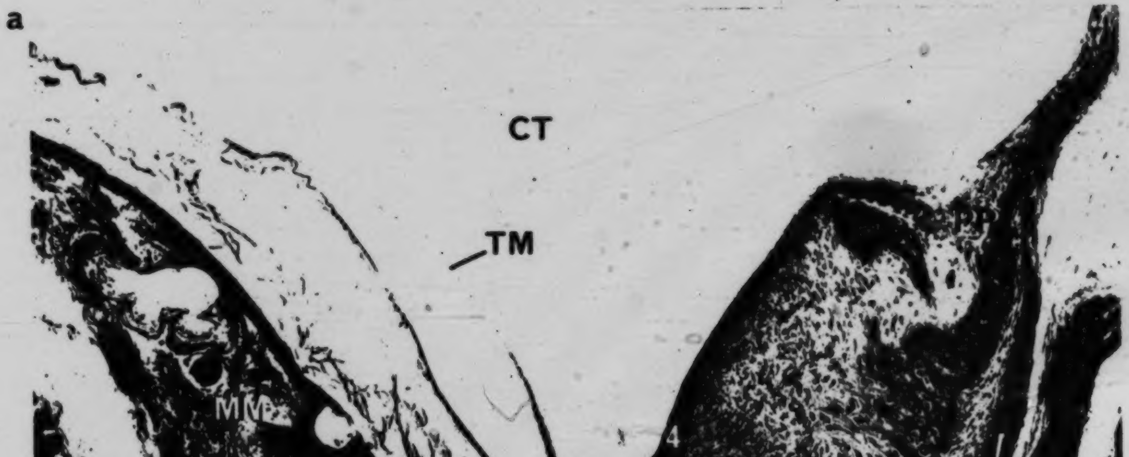
a. G. demidovii MPIH 1962/40 (newborn); s. 145/3, cross-section, right side; Azan; x 119.

b. L. tardigradus MPIH 1666 (near-term fetus); s. 617, cross-section, left side; Azan; x 34 and x 98.

Relationship of ectotympanic and petrosal plate II. Distinct, highly-fibrous uniting layers can be easily detected. They enclose, with the aid of the capsular layers of the ectotympanic and petrosal plate, a lighter-staining area which represents the middle layer. The definition and number of sutural tissues clearly contrasts with the state of sutural development seen in late fetal Microcebus.

1, capsular layer of petrosal plate; 2, capsular layer of ectotympanic; 3, middle layer; 4, uniting layer; 5, uniting layer (includes fibrous membrane of tympanic cavity).


Pr
TyM
CT
RTPP
FMTC


a
CT
TM
MM
4
3
2
5
E
FMTC

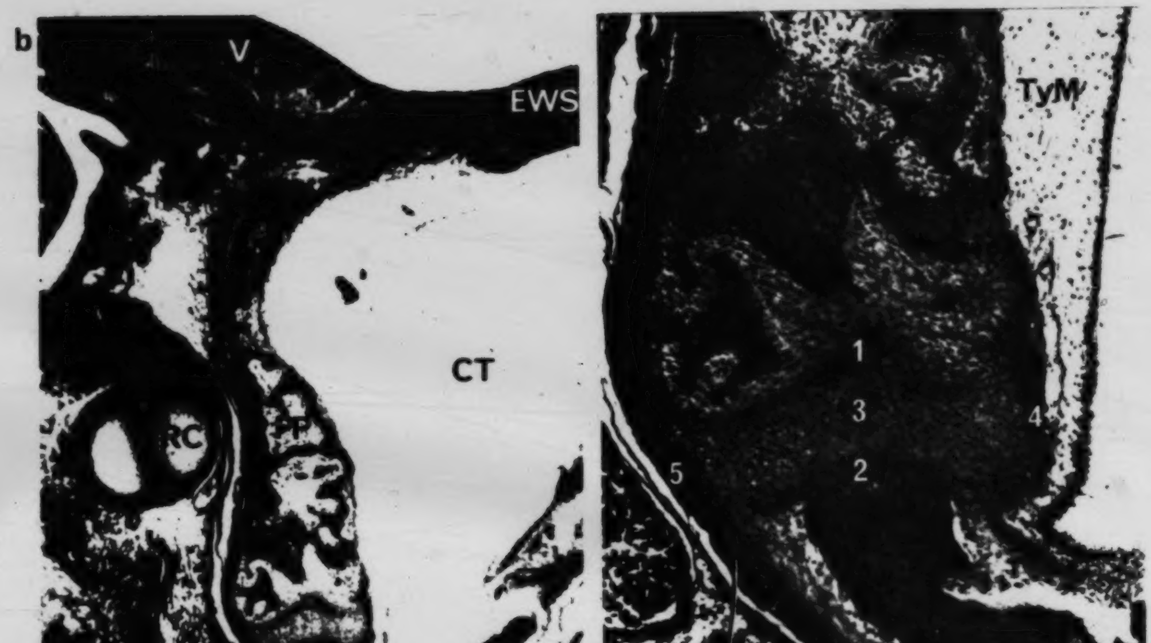

b
V
EWS
CT
RC
PP
E
TyM
1
3
2
4
5
EMTC

FIG. III-9 G. senegalensis MPIH 1967/117 (10 days old); s. 530, sagittal, left side; Azan; x 89.

Relationship of ectotympanic and petrosal plate III. Spicules of bone can be identified within the ectotympanic-petrosal plate suture. In the superior part of the suture, there is a complete bridge of bone joining the petrosal plate and ectotympanic. In the ventral part, the bridge is still incomplete. Situated between the spicules and grading histologically into them is a poorly-organized tissue which resembles cartilage (cf. Reichert's cartilage, lower right). This material conforms to the transitory tissue described by MOSS (1958) for the metopic suture of the rat. With fusion of the two bone territories, the ectotympanic-petrosal plate relationship has reached its definitive form.

Asterisks indicate spicules of bone within ectotympanic-petrosal plate suture.

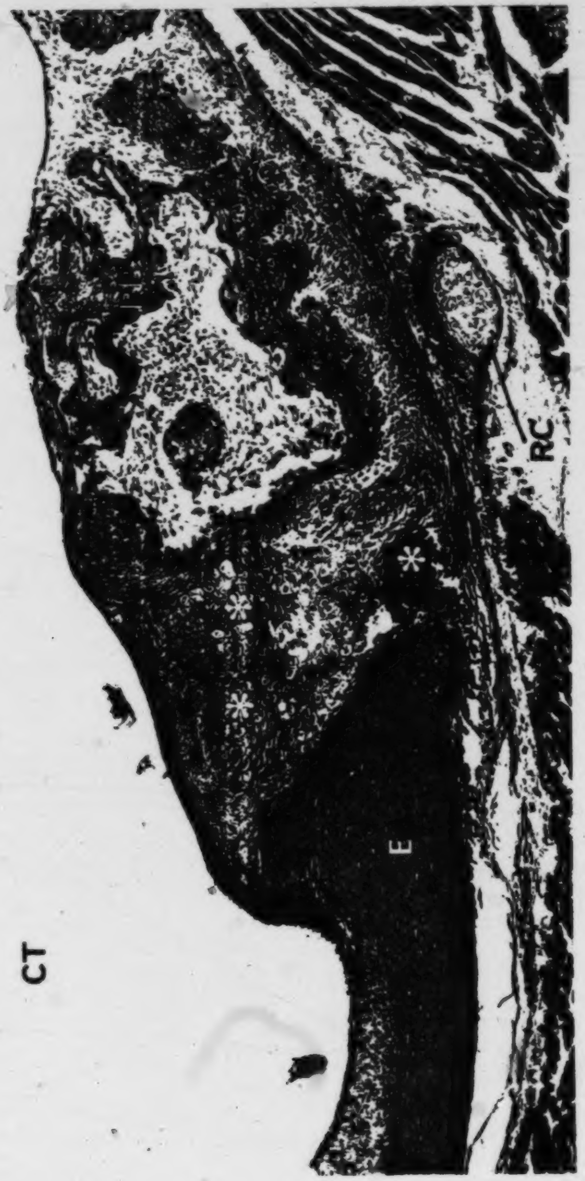

RC
*
*
*
E
CT

FIG. III-10 G. demidovii MPIH 102 (fetus); s. 531, cross-section, right side (sides rev.); Cresyl Violet; x 41.

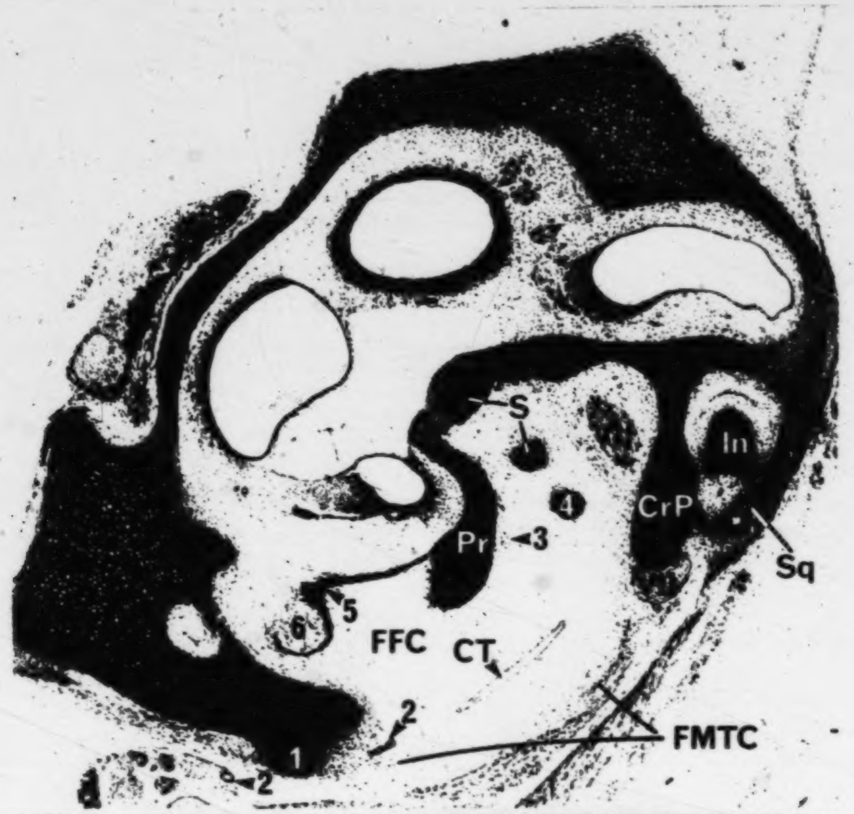
The end of the cochlear floor bears a small nodule of cartilage which represents the medial section of the caudal tympanic process of the petrosal. The cartilage composing this nodule is slightly younger than the rest of the cochlear floor.

1, medial section of the caudal tympanic process of the petrosal; 2, internal carotid a. and n.; 3, tympanic n.; 4, stapedius muscle; 5, secondary tympanic membrane; 6, perilymphatic duct; 7, internal jugular v.

FIG. III-11 G. demidovii MPIH 102 (fetus); s. 541, cross-section, right side (sides rev.); Cresyl Violet; x 45.

Directly behind the medial section of the caudal tympanic process of the petrosal, and joining the posterior end of the floor of the pars cochlearis to the anteroventral part of the pars canalicularis, is the processus recessus (future medial wall of the fossula fenestrae cochleae). The internal carotid a. enters the presumptive tympanic cavity beneath the processus recessus.

For key to numbered structures, see fig. III-10.


S
In
4
CrP
Pr
3
Sq
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6
FFC
CT
2
FMTC
1
2

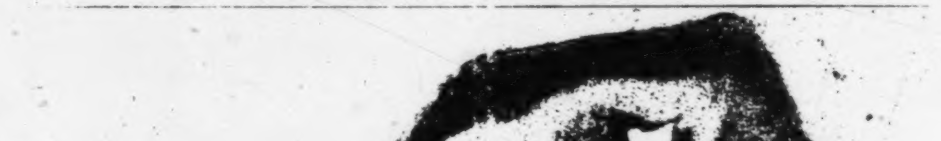

S
FIn
4
VII
Pr
3
6
CT
FMTC
PrR
7
2

FIG. III-12 G. demidovii MPIH 102 (fetus); s. 549, cross-section, left side; Cresyl Violet; x 45.

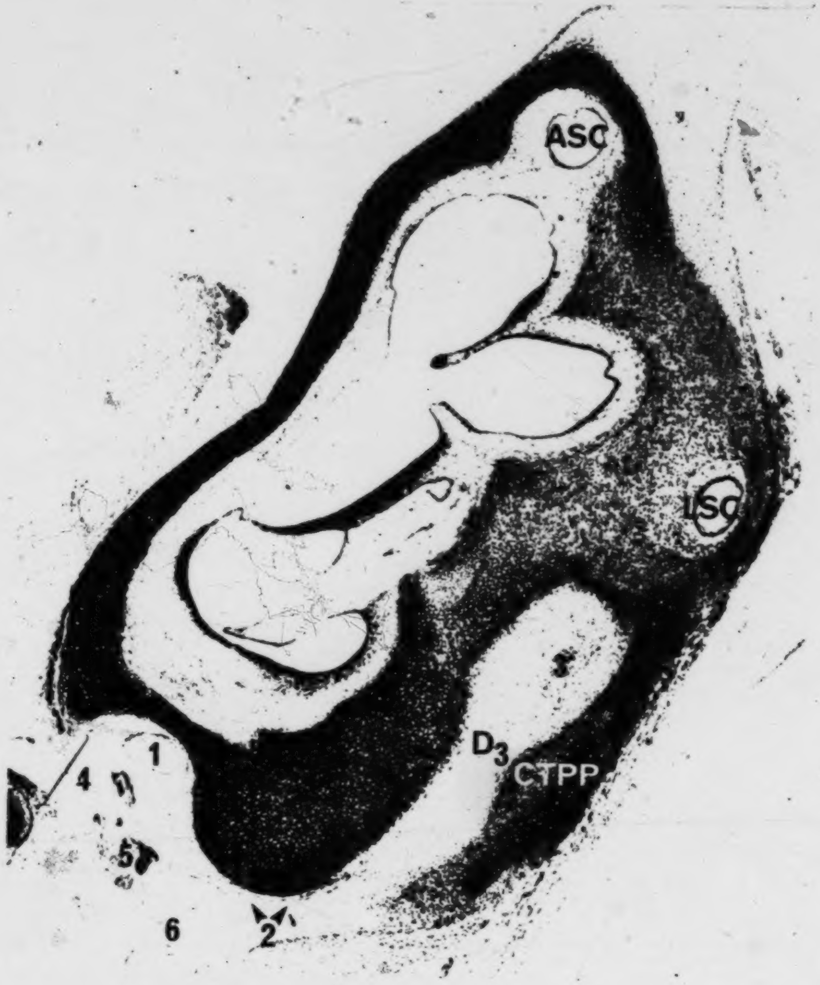
The crista parotica is continued posteriorly by the massive posterolateral section of the caudal tympanic process of the petrosal.

1, perilymphatic duct; 2, auricular ramus of the vagus entering rear of tympanic cavity; 3, stapedius m.; 4, fissura metotica; 5, IX and X nerves; 6, internal jugular v.

FIG. III-13 G. demidovii MPIH 120 (near-term fetus); s. 961, cross-section, left side; Cresyl Violet; x 33.

The anterior carotid enters a simple rete before passing into the cranial cavity. The branches of the rete rejoin, and the reconstituted anterior carotid (now as the cerebral carotid) receives the promontorial a. before reaching the circulus arteriosus.

1, rete of anterior carotid a.; 2, petro-occipital sinus; 3, cavernous sinus; 4, secondary cartilage in postglenoid process; 5, anterior carotid-promontorial a. anastomosis entering foramen caroticum primitivum; 6, promontorial a. joining anterior carotid a.; 7, nerves of pterygoid canal; 8, external jugular v.


ASC
LSC
D_3
CTPP
1
4
5
6
2

CS
Sq
V
AS
V
4
MC
E
BS
CAT
6
CT
2
1
E

FIG. III-14 G. demidovii MPIH 120 (near-term fetus); s. 1210, cross-section, left side; Cresyl Violet; x 28.

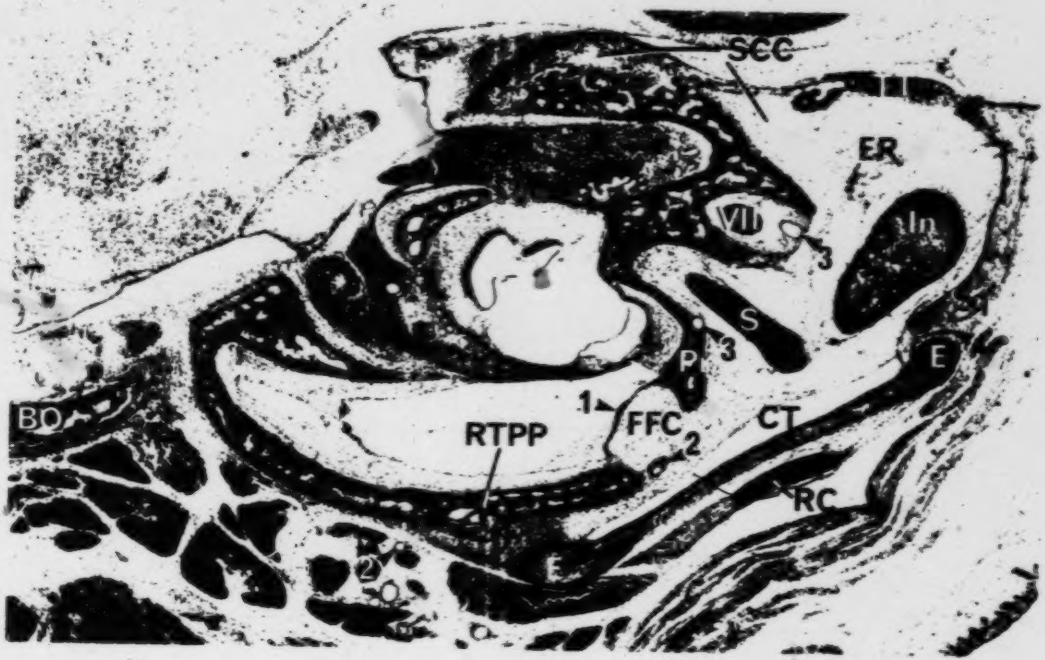
The supracochlear cavity originates as a dorsomedial diverticulum of the epitympanic recess which gradually inflates into the dorsal (cerebral) surface of pars cochlearis and, eventually, the anterior part of the petrosal plate.

1, secondary tympanic membrane; 2, internal carotid a. and n.;
3, stapedial a.; 4, chorda tympani; 5, tendon of stapedius m.

FIG. III-15 G. demidovii MPIH 120 (near-term fetus); s. 1237; cross-section, left side; Cresyl Violet; x 32.

The cartilaginous medial section of the caudal tympanic process of the petrosal is now partly surrounded by periosteal splints. These splints are in turn continuous with the trabeculae of the rostral tympanic process of the petrosal (see fig. III-1).

For key to numbered structures, see fig. III-14.


SCC
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VII
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RTPP
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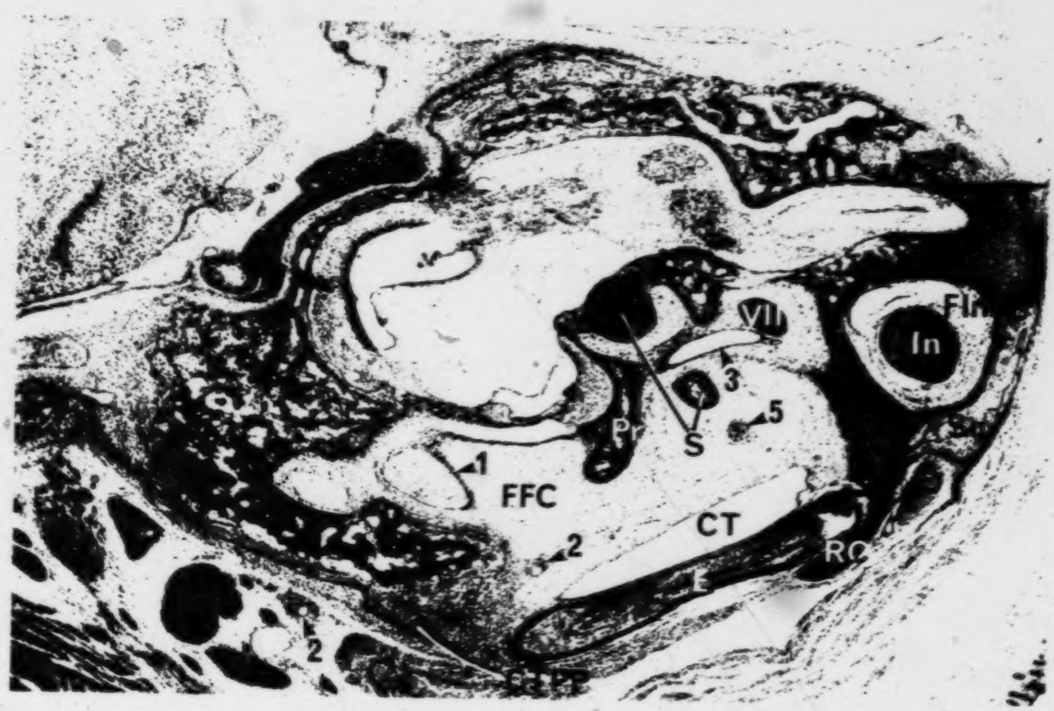
E


VII
FIn
In
3
S
5
P
1
FFC
CT
2
RC
E
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RTPP

FIG. III-16 G. demidovii MPIH 120 (near-term fetus); s. 1201, cross-section, right side; Cresyl Violet; x 32.

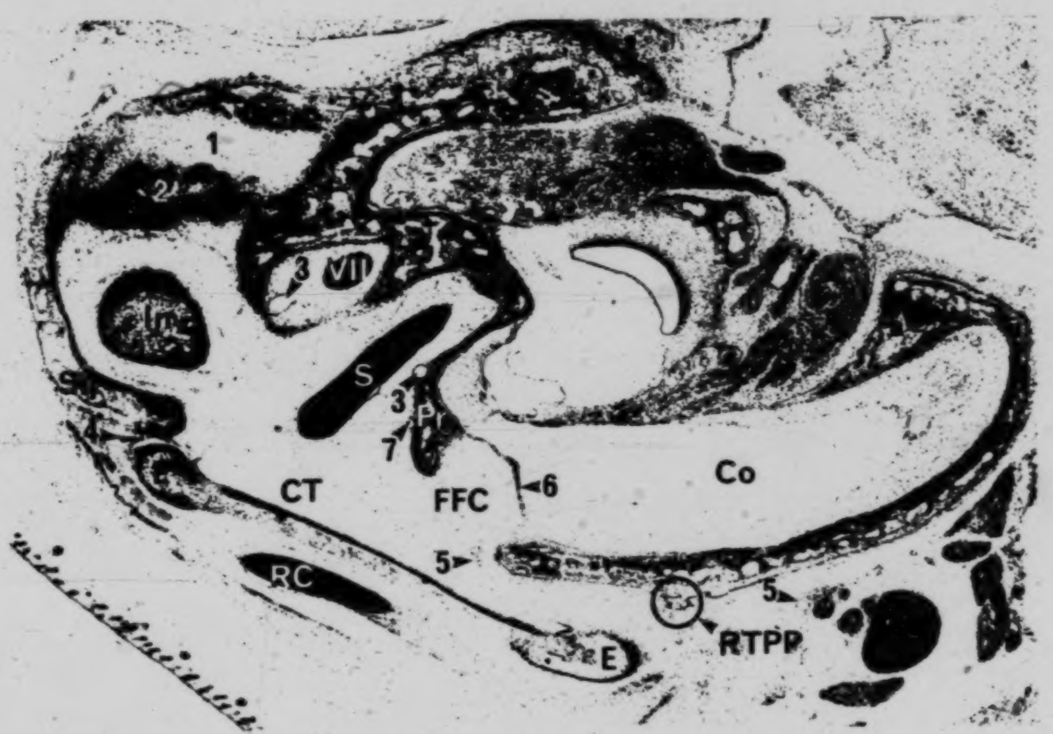
The root of the tegmen tympani and the adjacent part of the pars canaliculus have been excavated by pneumatic activity, partially exposing the wall of the lateral semicircular canal. Further pneumatization in this region produces the definitive aditus ad antrum and, later, the mastoid cavity (antrum and D_4).

1, area of excavation above lateral semicircular canal (future aditus); 2, wall of lateral semicircular canal; 3, stapedial a.; 4, chorda tympani; 5, internal carotid a. and n.; 6, secondary tympanic membrane; 7, tympanic n.

FIG. III-17 G. demidovii MPIH 120 (near-term fetus); s. 1243, cross-section, right side; Cresyl Violet; x 32.

The cartilaginous medial section of the caudal tympanic process of the petrosal is enclosed by periosteal splints (asterisks). Conditions in older specimens suggests that these splints do not continue to lay down bone in the cavity formed by the degeneration of the cartilage of the original medial section of the process. Instead, the splints become the side walls of a small diverticulum which opens into the tympanic cavity beneath the fossula fenestrae cochleae (see figs. III-22, III-23).

1, tympanic n.; 2, internal carotid a. and n.; 3, stapedius m.; 4, perilymphatic duct.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VII
In
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CT
FFC
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RTPP
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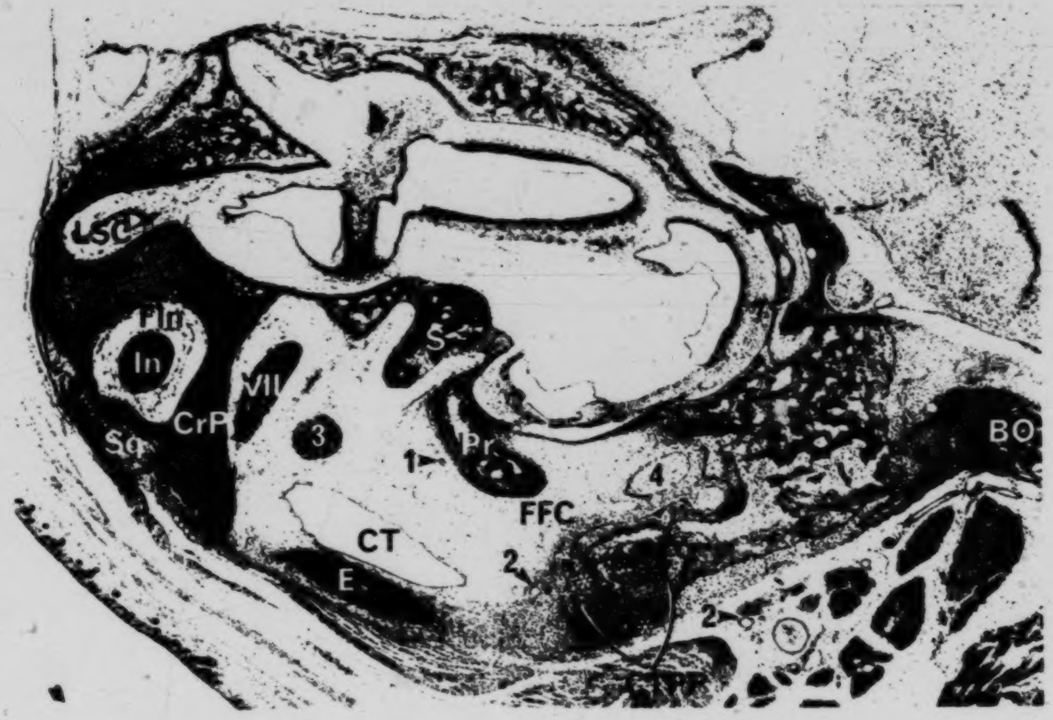
LSC
Pln
In
Sq
CrP
VII
3
S
Pr
1
FFC
4
BO
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2
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2

FIG. III-18 G. demidovii MPIH 120 (near-term fetus); s. 1258, cross-section, right side (sides rev.); Cresyl Violet; x 28.

A narrow cartilaginous bridge joins together the medial and posterolateral sections of the caudal tympanic process of the petrosal. This bridge helps define a long, slit-like foramen through which the internal carotid a. and the internal carotid, tympanic, and auricular ramus of the vagus nn. enter the presumptive tympanic cavity (see fig. III-1).

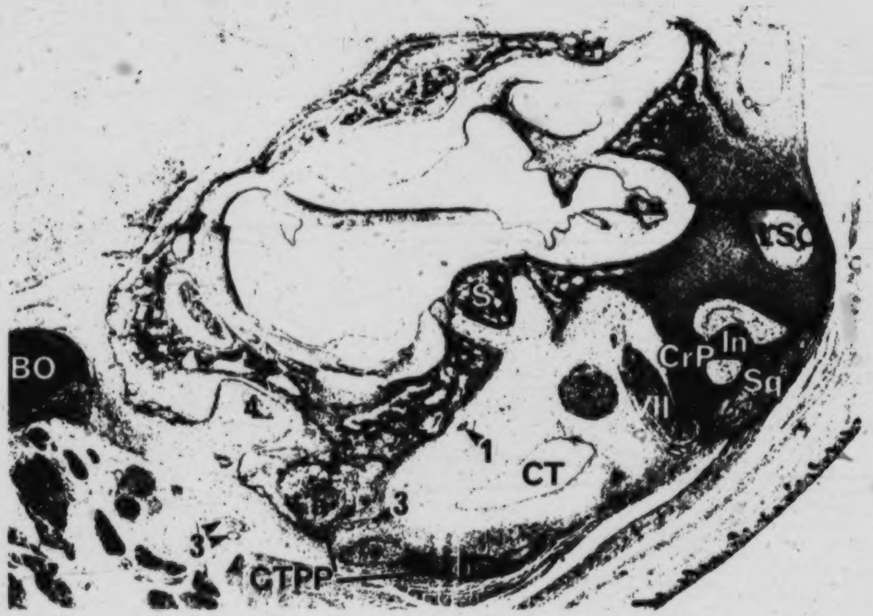
The letter 'a' indicates the medial, and the letter 'b' the posterolateral, sections of the CTPP. The cartilaginous bridge is identified by the asterisk.

1, tympanic n.; 2, stapedius m.; 3, internal carotid a. and n.; 4, perilymphatic duct; 5, auricular ramus of the vagus; 6, fissura metotica.

FIG. III-19 G. demidovii MPIH 120 (near-term fetus); s. 1285, cross-section, right side (sides rev.); Cresyl Violet; x 28.

The posterolateral section of the caudal tympanic process of the petrosal is mostly cartilaginous at this stage. It ossifies from a center in the anteroventral part of pars canalicularis.

For key to numbered structures, see fig. III-18.


rSC
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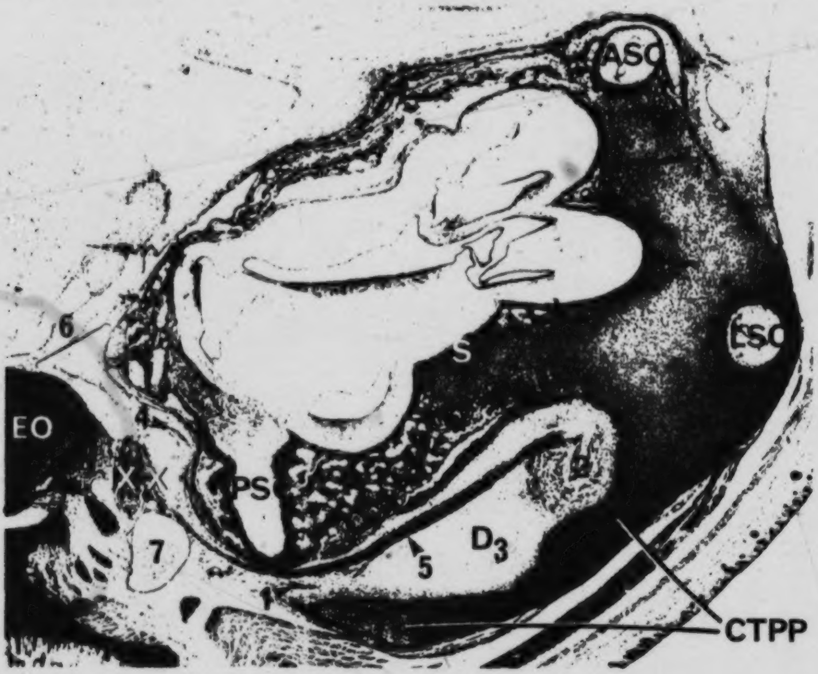
ASC
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6
EO
4
X
PS
D$_3$
5
7
CTPP

FIG. III-20 G. senegalensis MPIH 1962/40 (newborn); s. 133/1/1; cross-section, right side; Azan; x 28.

Anterior end of the tympanic cavity. The petrosal plate sends out a large lamina which forms the ventral part of the tubal canal. Note the participation of the alisphenoid (as the epitympanic wing of the sphenoid) in the roof of the tympanic cavity.

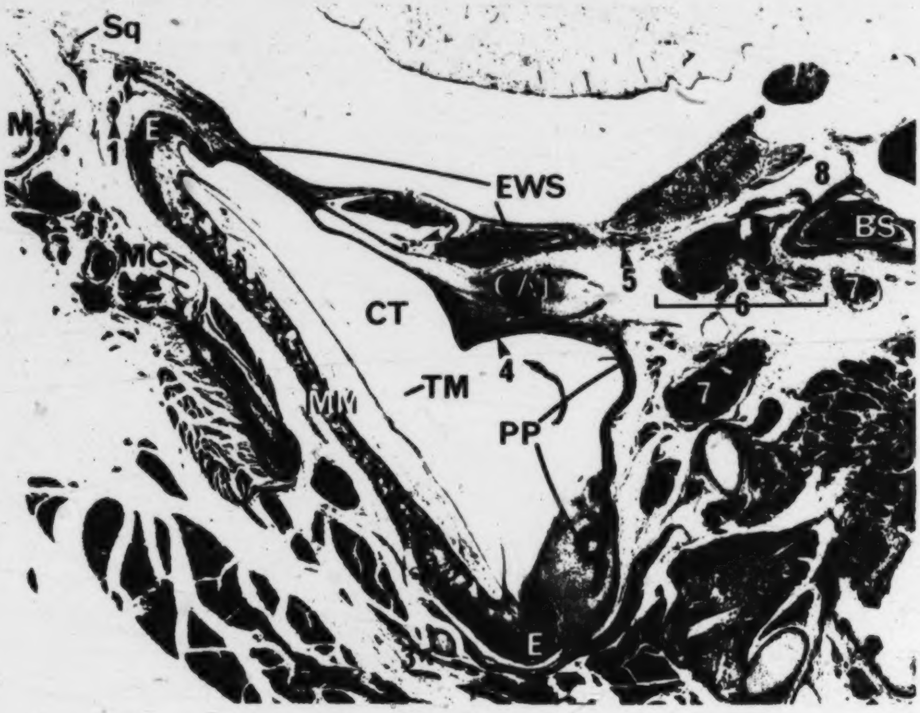
1, chorda tympani; 2, lesser petrosal n.; 3, Reichert's cartilage; 4, floor of tubal canal (formed by petrosal plate); 5, nerves of the pterygoid canal; 6, rete of the anterior carotid a.; 7, petro-occipital sinus; 8, cavernous sinus; 9, promontorial a. joining anterior carotid a.

2

FIG. III-21 G. senegalensis MPIH 1962/40 (newborn); s. 135/3, cross-section, right side; Azan; x 31.

The promontorial a. passes between the alisphenoid and the petrosal part of tubal canal in order to reach the anterior carotid beneath the anterior carotid foramen.

For key to numbered structures, see fig. III-20.


Sq
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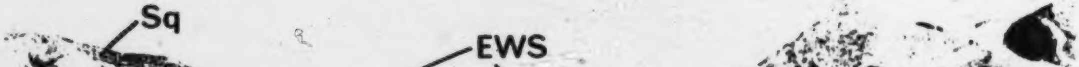
Sq
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CAT
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MC
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TM
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MM
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FIG. III-22 G. senegalensis MPIH 1962/40 (newborn); s. 193/2/1, cross-section, right side; Azan; x 28.

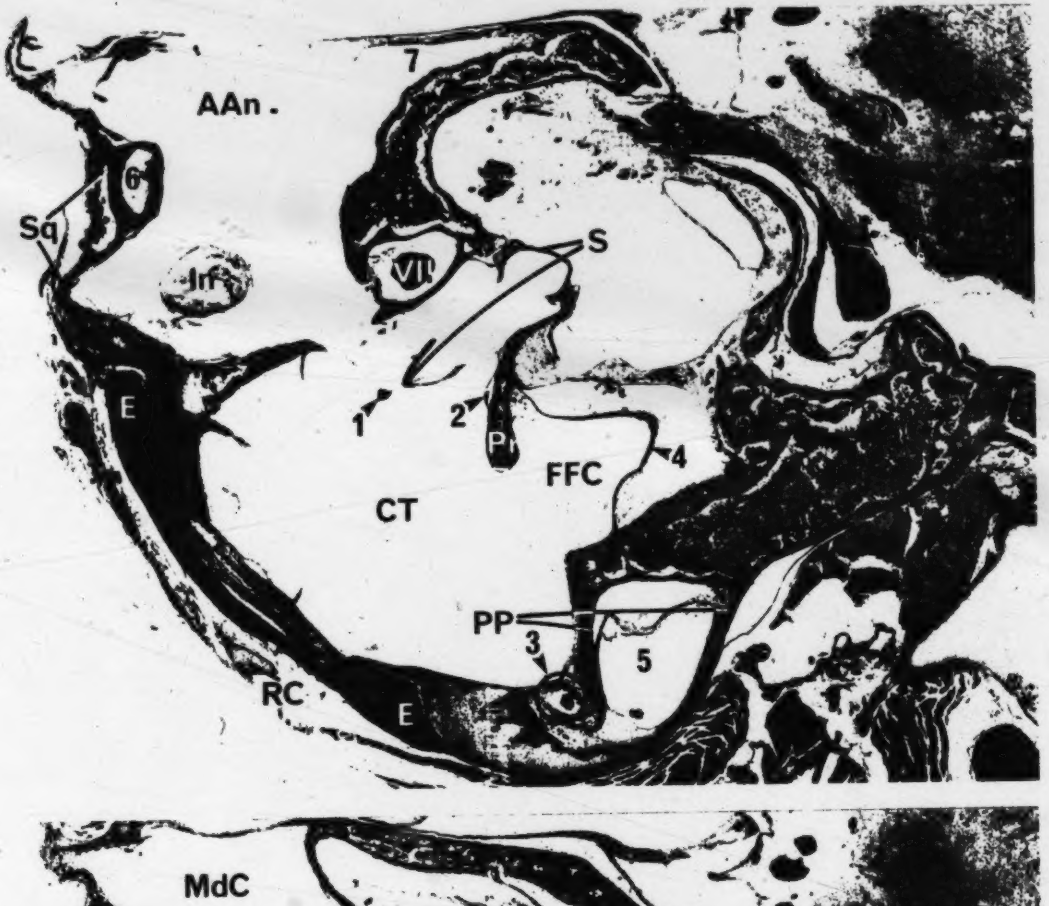
The small diverticulum (5) beneath the fossula fenestra cochleae is not part of the developing medial accessory cavity, despite the appearance of this section. The diverticulum is continuous with the tympanic cavity and derived from the medial section of the original CTPP (see fig. III-17). It is wide but very short; it terminates only a few micra posterior to this section (see fig. III-23). In the adult (fig. III-2) this diverticulum is visible as a small indentation of the lateral lamella of the petrosal plate ('longitudinal septum'). The true medial accessory cavity will later expand into the medial sidewall of the diverticulum.

1, tendon of stapedius m.; 2, tympanic n.; 3, internal carotid a. entering tympanic cavity through posterior carotid foramen; 4, secondary tympanic membrane; 5, diverticulum; 6, sidewall of lateral semicircular canal; 7, posterior end of supracochlear cavity.

FIG. III-23 G. senegalensis MPIH 1962/40 (newborn); s. 196/2/3, cross-section, right side; Azan; x 28.

The mastoid cavity is undergoing rapid development in this specimen (see also figs. III-24, III-25).

For key to numbered structures, see fig. III-22.


7
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VII
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FFC
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RC
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MdC
LSC
FIn
VII
S
S
In
1
2
Pr
FFC
4
EO
CT
RC
PP
3

FIG. III-24 G. senegalensis MPIH 1962/40 (newborn); s. 198/1/2, cross-section, left side; Azan; x 28.

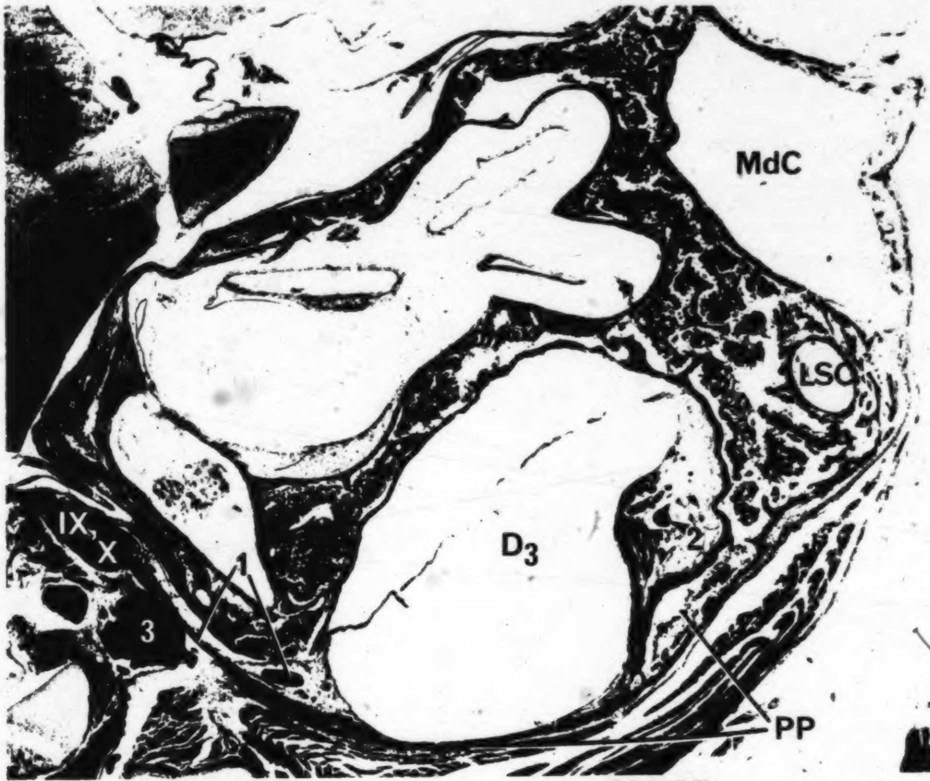
Mastoid cavity and posterior end of the tympanic cavity (D_3). The mastoid cavity is still expanding rapidly, unlike the ventral wall of D_3. The auricular ramus of the vagus appears twice in this section (see also fig. III-25) because it travels around the posterior wall of D_3 before proceeding anteriorly.

1, auricular ramus of vagus and tympanic nn. entering posterior end of tympanic cavity; 2, auricular ramus of vagus n. passing through fossa for stapedius m.; 3, internal jugular v.

FIG. III-25 G. senegalensis MPIH 1962/40 (newborn); s. 204/2/1, cross-section, left side; Azan; x 28.

Mastoid cavity and posterior end of tympanic cavity (D_3).

For key to numbered structures, see fig. III-24.


MdC
LSC
IX, X
D3
1
2
3
PP

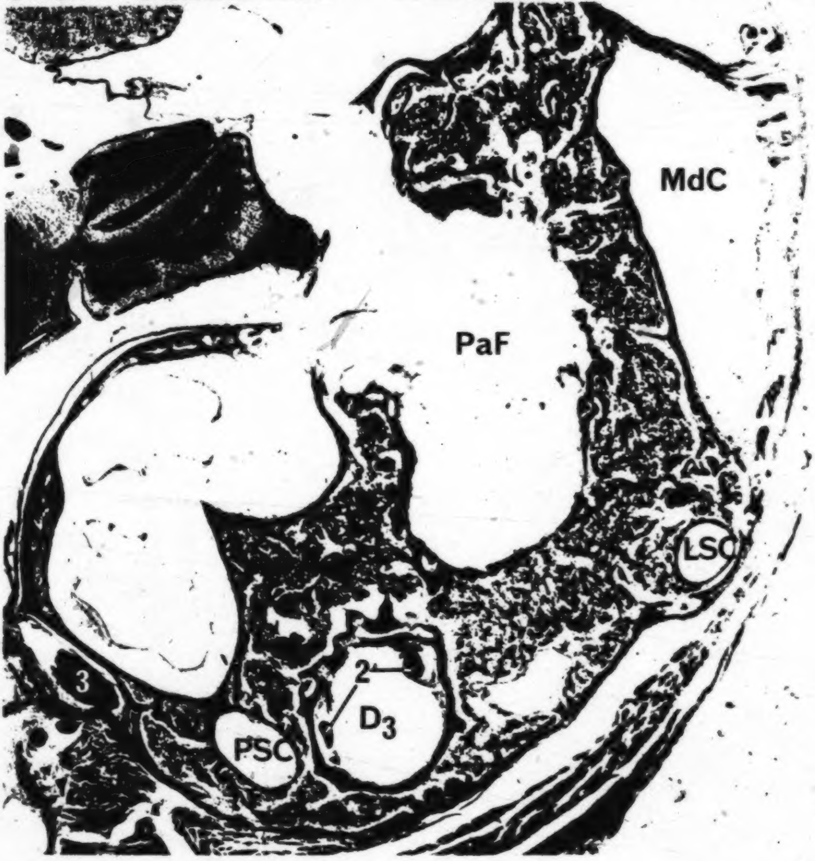

MdC
PaF
LSC
3
2
D3
PSC

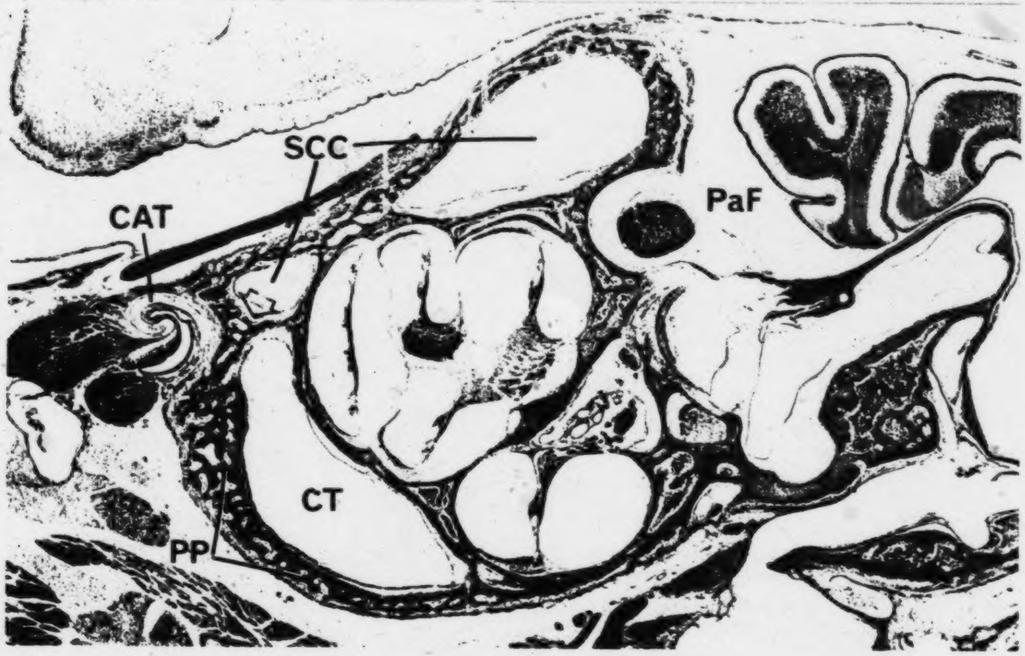
FIG. III-26 G. senegalensis MPIH 1967/117 (10 days old); s. 670, sagittal section, left side; Azan; x 18.

Section through medial part of auditory capsule. The supracochlear cavity reaches the anterior end of pars cochlearis and then penetrates the petrosal plate. Inflation of the petrosal plate has just begun in this specimen (direction indicated by outline arrow).

FIG. III-27 G. senegalensis MPIH 1967/117 (10 days old); s. 570, sagittal section, left side; Azan; x 16.

Section through central part of auditory capsule. The supracochlear cavity inflates the whole dorsal (cerebral) surface of the pars cochlearis. The mastoid cavity eventually isolates the parafloccular fossa from the sidewall of the skull.

1, anterior semicircular canal; 2, posterior semicircular canal; 3, ampullar end of posterior semicircular canal; 4, tensor tympani m.; 5, facial n.


SCC
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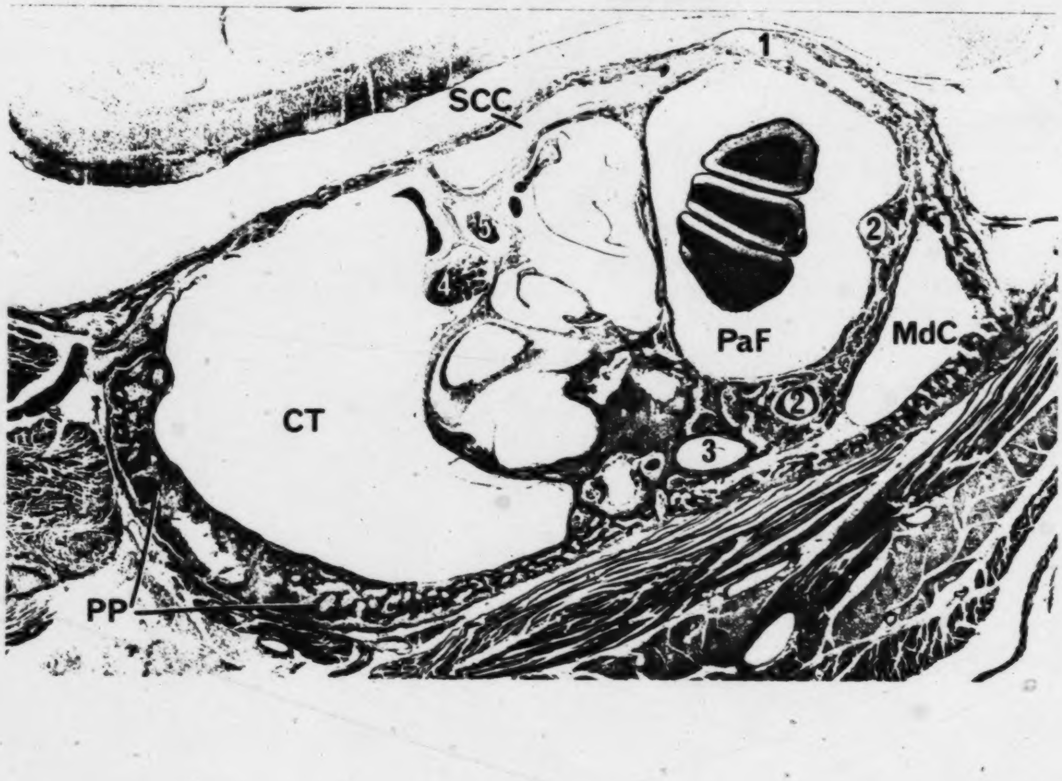
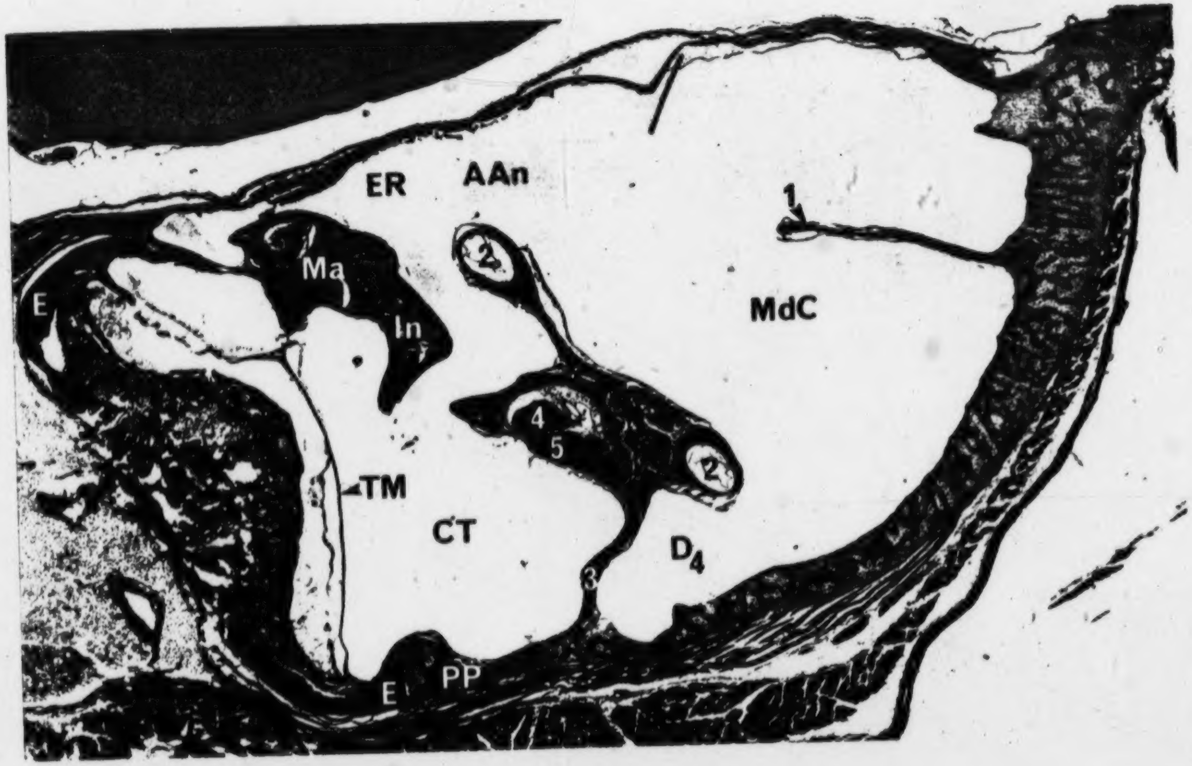

1
SCC
5
4
2
PaF
MdC
2
CT
3
PP

FIG. III-28 G. senegalensis MPIH 1967/117 (10 days old); s. 440, sagittal section, left side; Azan; x 18.

Section through lateral part of auditory capsule. This section illustrates the relationship of the true tympanic cavity, epitympanic recess, and mastoid cavity to each other and to other parts of the middle ear. Diverticulum D_4 is the ventromedial extension of the mastoid cavity which extends into the posterior part of the petrosal plate in postnatal life. Pneumatic effects are already visible, for only a thin plate of bone (3) lies between the tympanic cavity and D_4.

1, septum within mastoid cavity; 2, lateral semicircular canal; 3, posterior wall of tympanic cavity; 4, facial n.; 5, stapedius m.


ER
AAn
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MdC
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In
2
4
5
2
TM
CT
3
D$_4$
E
PP

FIG. III-29 *Tarsius bancanus* MPIH 1963/13 (adult); s. 1825, cross-section, left side; Azan; x 172.

In *Tarsius*, as in *Galago*, the bone of the ectotympanic remains intermediate in architecture after fusion with the petrosal plate. Despite the appearance of this section, the petrosal plate does not actually overgrow the ectotympanic. New bone of the mature, lamellated type is laid down laterally over the original ectotympanic, this obscures the position of the ectotympanic-petrosal plate suture in the adult.

The white outline arrows indicate the border between intermediate and lamellated bone in this section.

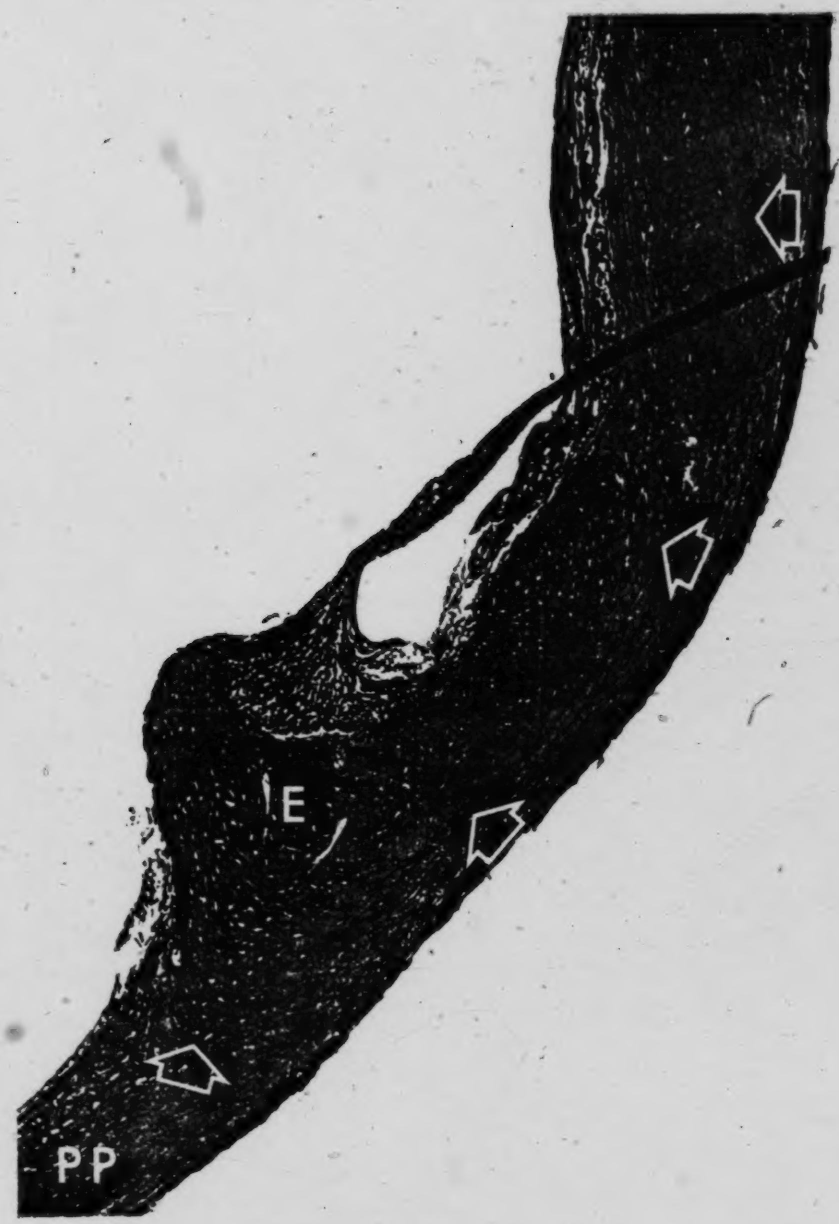

E
PP

FIG. III-30 Auditory region of a 27 mm HL Loris tardigradus, alizarin preparation; after RAMASWAMI (1957). Only bony areas are stained.

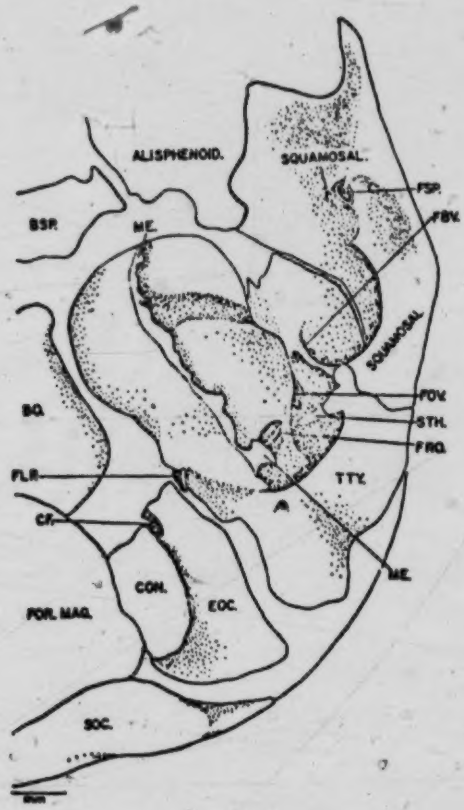
The 'mastoid extension' is equivalent to the rostral tympanic process of the petrosal and the medial section of the caudal tympanic process of the petrosal. The posterolateral section of the caudal tympanic process is identified by the asterisk (*).

BO., basioccipital; BSP., basisphenoid; CF., hypoglossal foramen; CON., occipital condyle; EOC., exoccipital; FBV., stapedial foramen; FLP., posterior lacerate foramen; FOR. MAG., foramen magnum; FOV., apertura fenestrae vestibuli; FRO., apertura fossulae fenestrae cochleae; FSP., postglenoid foramen; ME., 'mastoid extension'; SOC., supraoccipital; STH., stylohyal.

FIG. III-31 Auditory regions of 'juvenile' specimens of Perodicticus potto and Loris tardigradus; after VAN KAMPEN (1905); x 3.5.

The medial half of the promontory is still exposed ventrally in these specimens, no doubt due to the small size of the medial accessory cavity in young lorises.

a.s., alisphenoid; a.t., ectotympanic; b., petrosal bulla (petrosal plate); b.o., basioccipital; e.o., exoccipital; f.c., anterior carotid foramen; f.c.e., posterior carotid foramen; f. md., mandibular fossa; f.g., postglenoid foramen; f.o., foramen ovale; f.s., stylomastoid foramen; m., mastoid region; m.t., tympanic membrane; p.p., promontory or pars cochlearis; t., ectotympanic.


ALISPHENOID.
SQUAMOSAL.
FSP.
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BSP.
ME.
SQUAMOSAL.
BO.
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STH.
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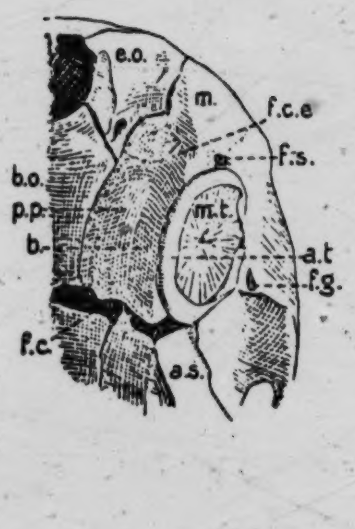
FLR.
TTY.
A
CF.
ME.
CON.
EOC.
FOR. MAG.
SOC.
mm


e.o.
m.
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f.s.
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p.p.
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a.t
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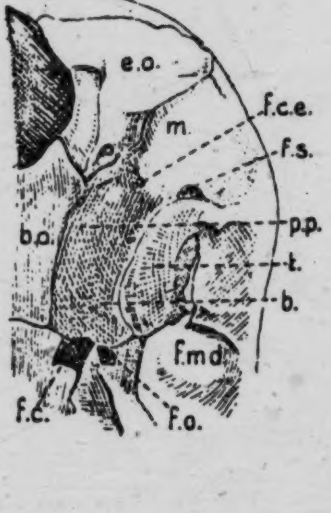
f.c.
a.s.


e.o.
m.
f.c.e.
f.s.
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b.o.
t.
b.
f.md.
f.c.
f.o.

FIG. III-32 L. tardigradus MPIH 1666 (near-term fetus); s. 719, cross-section, right side; Azan; x 25.

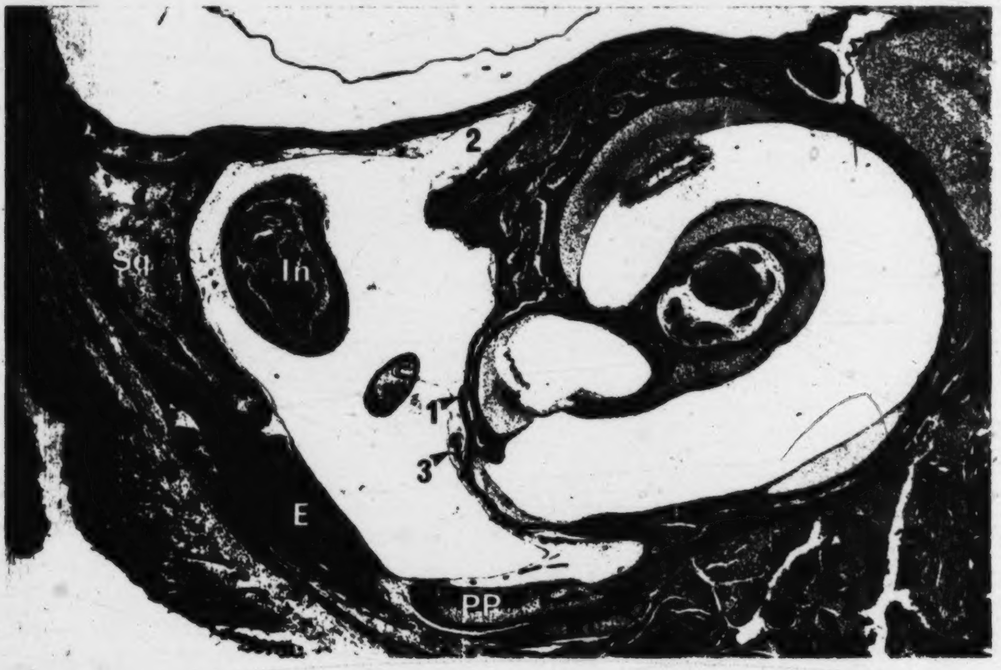
Developing supracochlear cavity.

1, stapedial a.; 2, developing supracochlear cavity; 3, internal carotid a. and n.

FIG. III-33 L. tardigradus MPIH 1666 (near-term fetus); s. 737, cross-section, right side; Azan; x 25.

Loris lacks the small diverticulum beneath the fossula fenestrae cochleae which is found in Galago (cf. fig. III-22). The developing antrum has already attained large size.

1, stapedial a.; 2, supracochlear cavity; 3, internal carotid n. and tympanic n.; 4, internal carotid a.; 5, sidewall of lateral semicircular canal; 6, secondary tympanic membrane.


2
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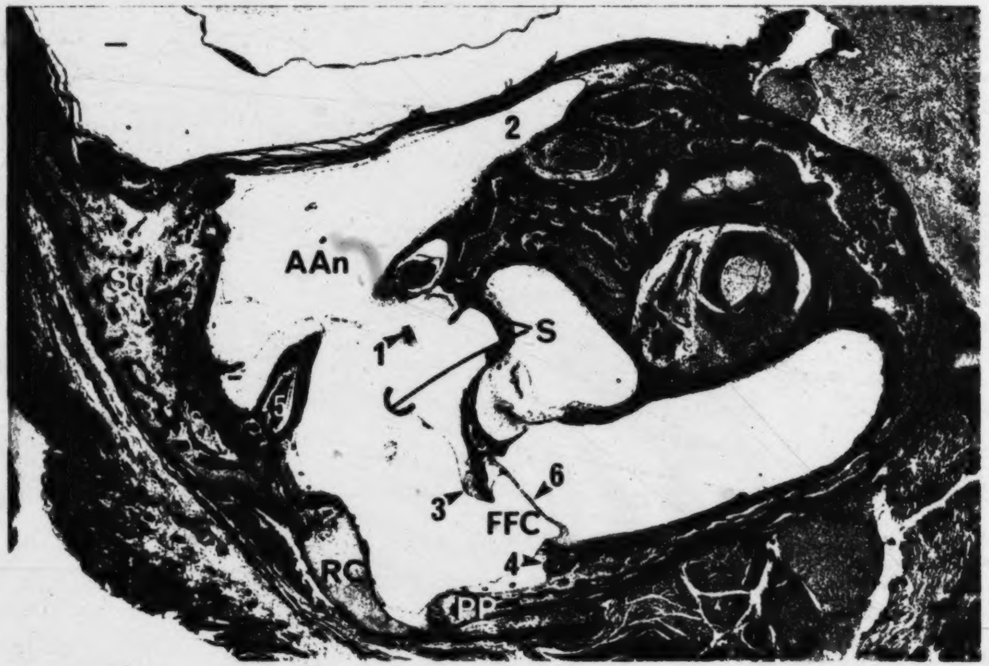
2
Sq
AAn
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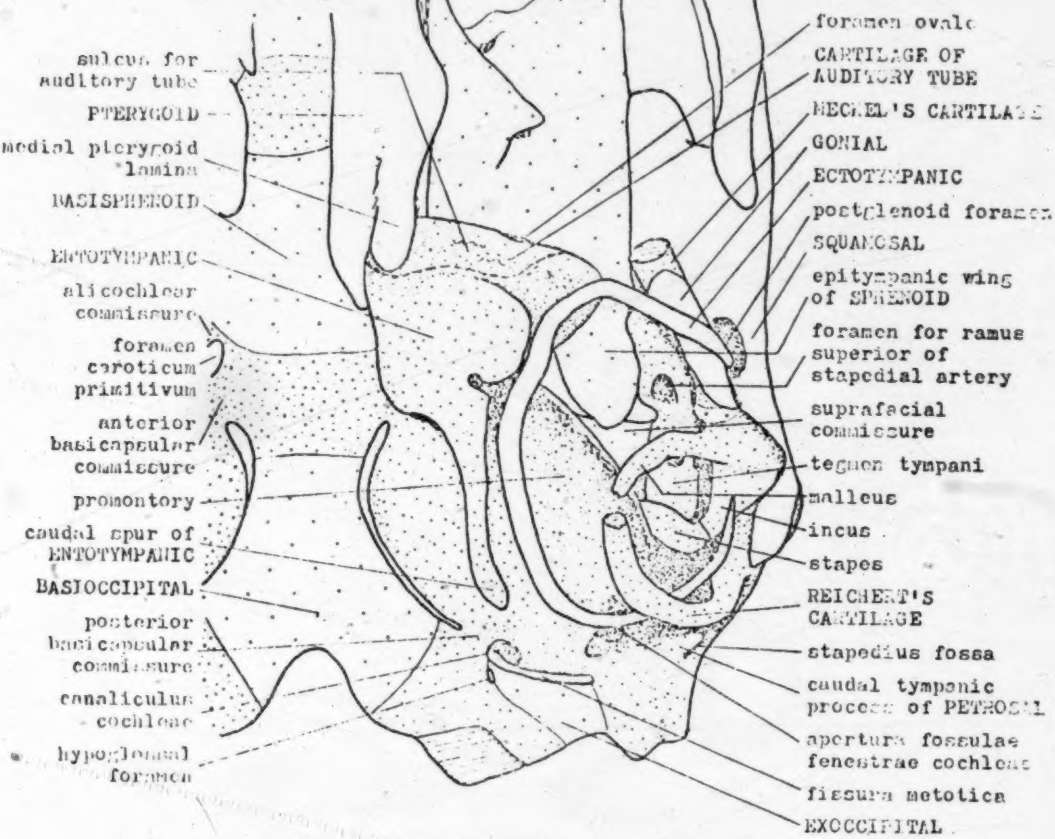
FFC
4
RC
PP

FIG. IV-1 *T. glis* MPIH 1959/4 (near-term fetus). Reconstruction of left auditory region and associated structures, ca. x 12 (after SPATZ 1966).

It is not possible to subdivide precisely the anterior mass of cartilage into separate tubal and entotympanic components. The dashed line, however, roughly indicates where the boundary between the two probably lies. The chief feature of this stage is the long caudal spur of the entotympanic which grows within the fibrous membrane of the tympanic cavity.

FIG. IV-2 *T. glis* MPIH 1960/77 (newborn). Reconstruction of left auditory region and associated structures, ca. x 12 (after SPATZ 1966).

The entotympanic has fused with the auditory capsule in two places: anteriorly with the tegmen tympani (*) and posteriorly with the tympanic process of the petrosal (**). Additionally, the caudal spur has broadened considerably and now covers a large portion of the ectotympanic--rendering it partially aphaneric.


sulcus for auditory tube
PTERYGOID
medial pterygoid lamina
BASISPHENOID
ENTOTYMPANIC
alicochlear commissure
foramen caroticum primitivum
anterior basicapsular commissure
promontory
caudal spur of ENTOTYMPANIC
BASIOCCIPITAL
posterior basicapsular commissure
canaliculus cochleae
hypoglossal foramen
foramen ovale
CARTILAGE OF AUDITORY TUBE
MECKEL'S CARTILAGE
GONIAL
ECTOTYMPANIC
postglenoid foramen
SQUAMOSAL
epitympanic wing of SPHENOID
foramen for ramus superior of stapedial artery
suprafacial commissure
tegmen tympani
malleus
incus
stapes
REICHERT'S CARTILAGE
stapedius fossa
caudal tympanic process of PETROSAL
apertura fossulae fenestrae cochleae
fissura metotica
EXOCCIPITAL

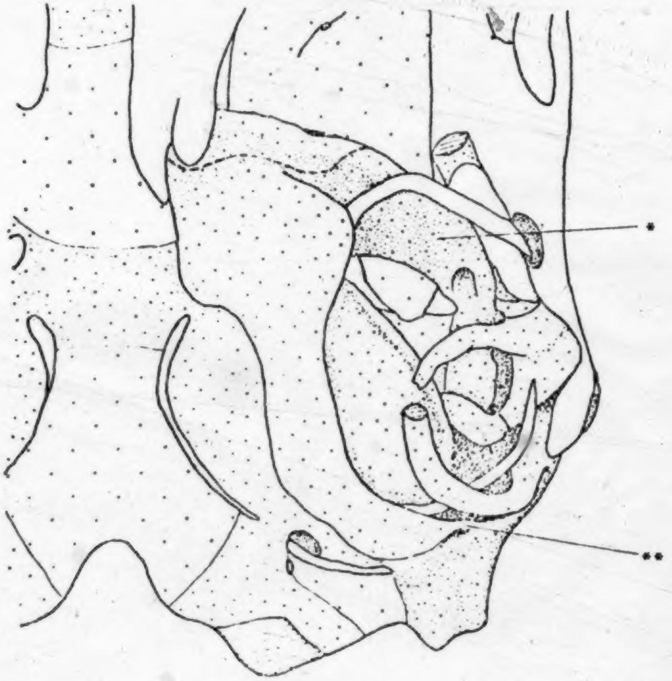
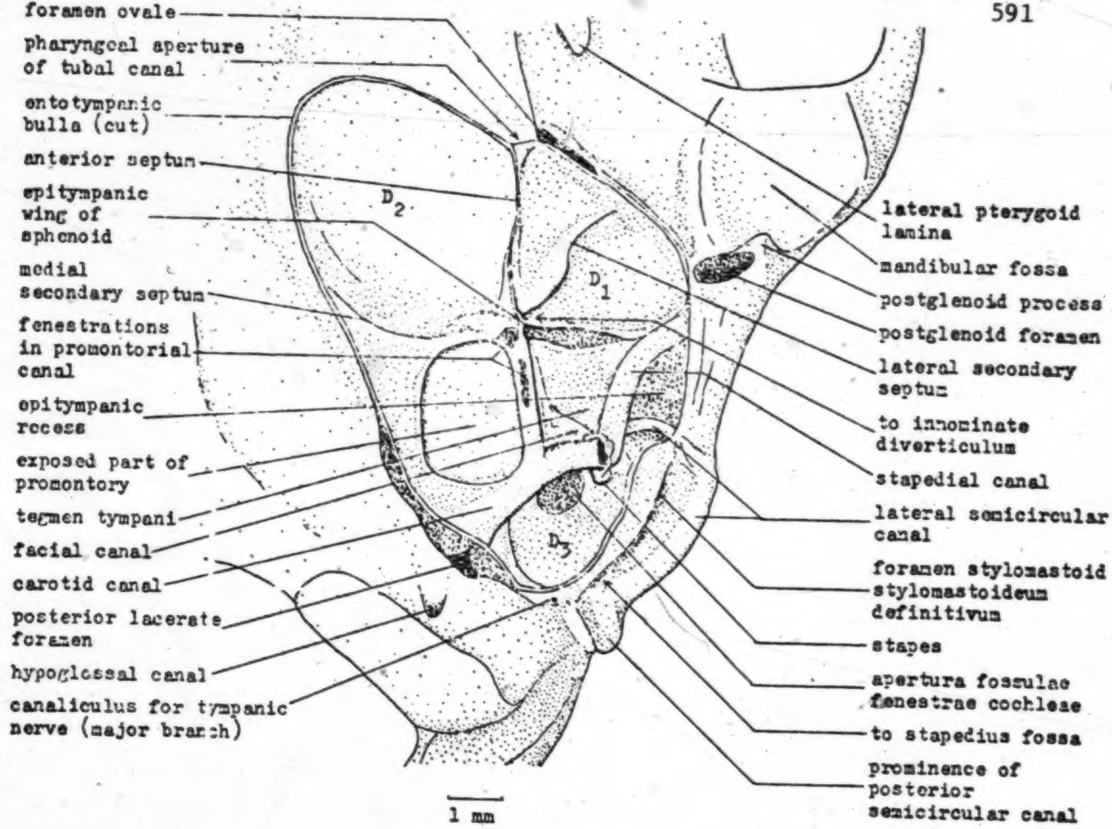

*
**

FIG. IV-3 *T. glis* adult. General view of left auditory region, ventral aspect.

The ectotympanic and most of the ventral part of the entotympanic (which forms the bulla proper) has been removed. This figure should be compared to fig. IV-4.

FIG. IV-4 *T. glis* adult. Further dissection of the left auditory region of the same specimen illustrated in fig. IV-3.

The entire entotympanic has been removed except for the part covering the internal carotid artery and the medial section of diverticulum D_3. The true extent of the epitympanic wing of the sphenoid, the small epitympanic wing of the petrosal, and the persistent piriform fenestra are now revealed. Removal of the dorsal parts of the entotympanic also clearly exposes the almost-complete ring of small cristae which externally buttress the bulla.


foramen ovale
pharyngeal aperture of tubal canal
entotympanic bulla (cut)
anterior septum
epitympanic wing of sphenoid
medial secondary septum
fenestrations in promontorial canal
epitympanic recess
exposed part of promontory
tegmen tympani
facial canal
carotid canal
posterior lacerate foramen
hypoglossal canal
canaliculus for tympanic nerve (major branch)
D_2
D_1
D_3
1 mm
lateral pterygoid lamina
mandibular fossa
postglenoid process
postglenoid foramen
lateral secondary septum
to innominate diverticulum
stapedial canal
lateral semicircular canal
foramen stylomastoid stylomastoideum definitivum
stapes
apertura fossulae fenestrae cochleae
to stapedius fossa
prominence of posterior semicircular canal

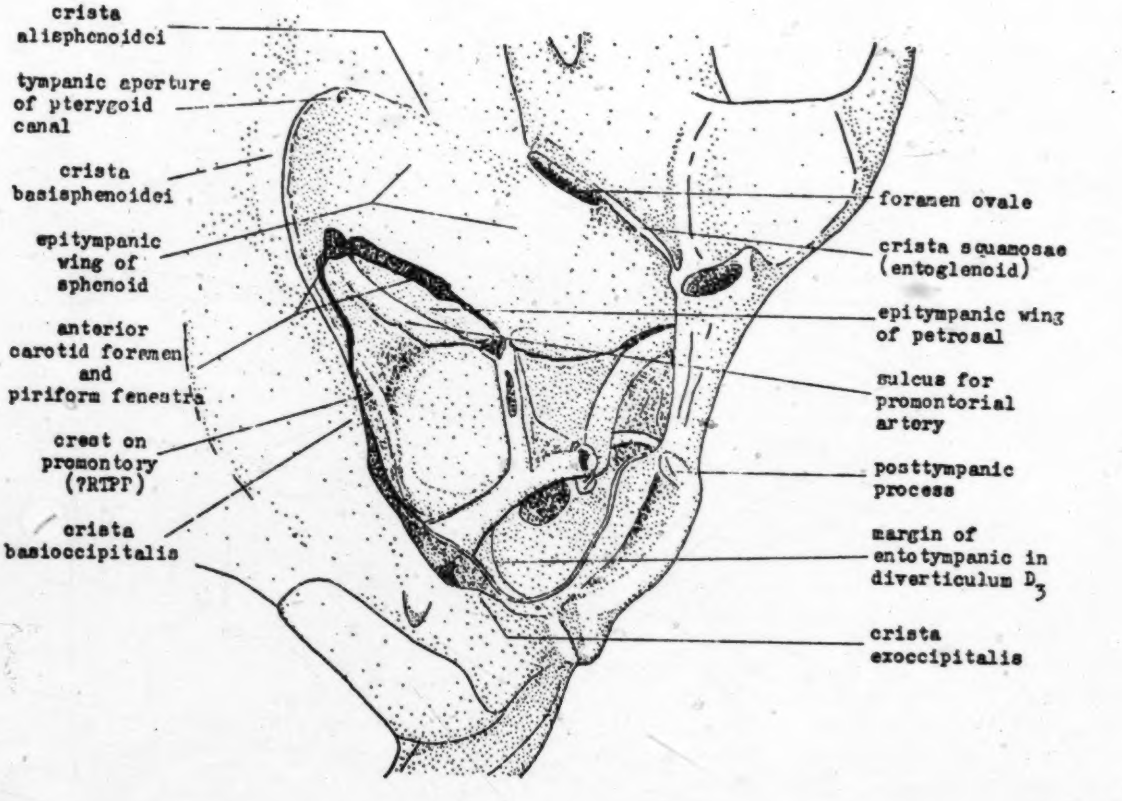
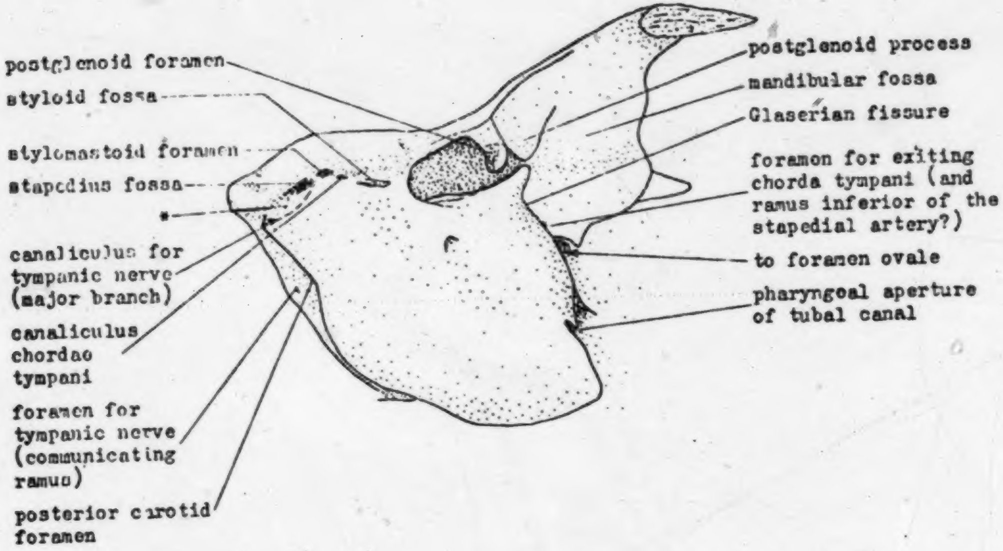

crista alisphenoidei
tympanic aperture of pterygoid canal
crista basisphenoidei
epitympanic wing of sphenoid
anterior carotid foramen and piriform fenestra
crest on promontory (?RTPP)
crista basioccipitalis
foramen ovale
crista squamosae (entoglenoid)
epitympanic wing of petrosal
sulcus for promontorial artery
posttympanic process
margin of entotympanic in diverticulum D_3
crista exoccipitalis

FIG. IV-5 *T. glis* adult. Right auditory region, ventrolateral aspect (after SABAN 1963).

The area bordered by the dashed line (*) represents the probable maximum extent of the caudal tympanic process of the petrosal in the adult.

FIG. IV-6 Major arteries and nerves of the middle ear in *T. glis* (semidiagrammatic).

1, promontorial artery (to circulus arteriosus); 2, nerves of the pterygoid canal (deep petrosal and greater petrosal); 3, greater petrosal nerve (to pterygopalatine ganglion); 4, lesser petrosal nerve (to otic ganglion); 5, ramus inferior of the stapedial artery (to 'internal' maxillary artery); 6, tympanic plexus; 7, canal for proximal part of stapedial artery; 8, ramus superior of stapedial artery (middle meningeal); 9, medial branch of internal carotid nerve; 10, lateral branch of internal carotid nerve; 11, tympanic nerve (major branch); 12, inferior tympanic artery; 13, stapes; 14, apertura fossulae fenestrae cochleae; 15, chorda tympani (to lingual nerve); 16, facial (VII) nerve; 17, internal carotid artery; 18, stem of internal carotid nerve; 19, tympanic nerve (communicating ramus); 20, auricular ramus of vagus nerve.


postglenoid foramen
styloid fossa
stylomastoid foramen
stapedius fossa
*
canaliculus for tympanic nerve (major branch)
canaliculus chordae tympani
foramen for tympanic nerve (communicating ramus)
posterior carotid foramen
postglenoid process
mandibular fossa
Glaserian fissure
foramen for exiting chorda tympani (and ramus inferior of the stapedial artery?)
to foramen ovale
pharyngeal aperture of tubal canal

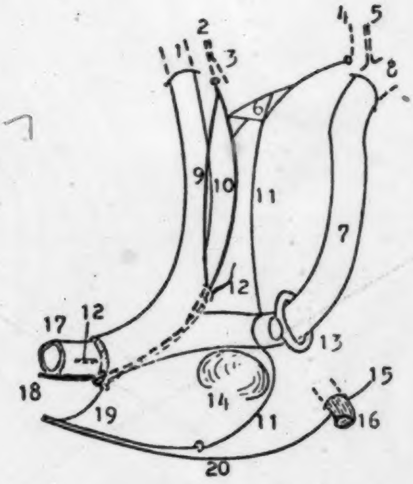

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FIG. IV-7 T. glis MPIH 1960/82a (near-term fetus); s. 1050, cross-section, right side (sides rev.); Azan; x 31.

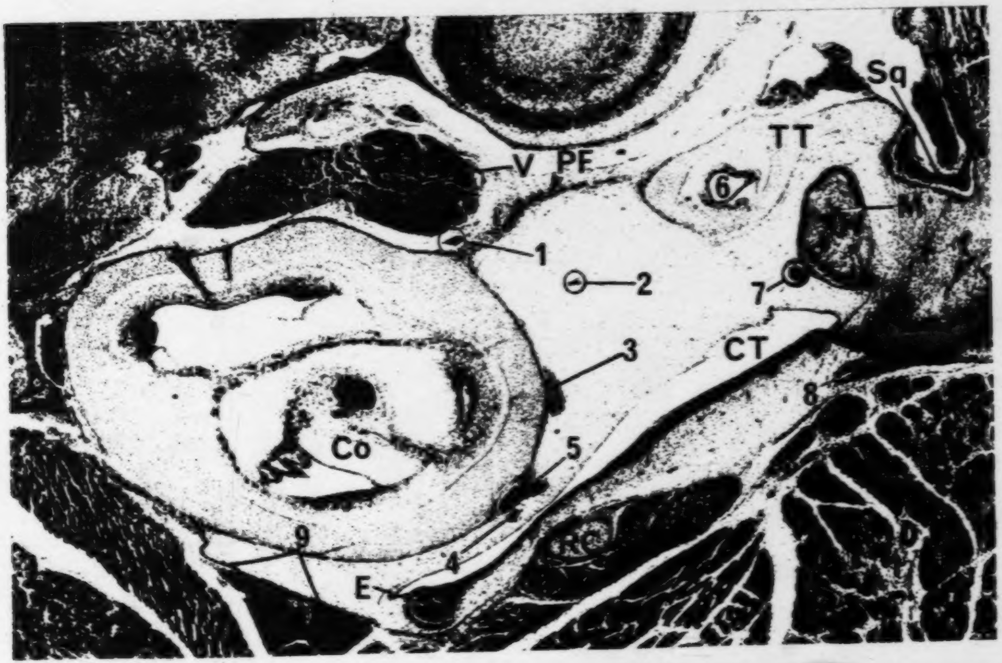
Growth of the entotympanic I. At this stage the ventral wall is almost entirely membranous. The anterior mass of cartilage (presumably consisting of both tubal and entotympanic material) is present, but it is limited to the anterior part of the presumptive tympanic cavity and does not appear in this section.

1, greater petrosal n.; 2, tympanic n. (major branch); 3, internal carotid n. (lateral branch); 4, internal carotid n. (medial branch); 5, promontorial a.; 6, (proximal) stapedial a.; 7, chorda tympani; 8, auricular cartilage; 9, FMTC.

FIG. IV-8 T. glis MPIH 1959/4; s. 336/2, cross-section, left side; Azan; x 27.

Growth of the entotympanic II. A lengthy caudal spur, presumably consisting only of entotympanic material, has grown out from the anterior mass of cartilage within the fibrous membrane of the tympanic cavity (cf. figs. IV-1, IV-12).

1, greater petrosal n.; 2, tympanic n. (major branch); 3, promontorial a.; 4, internal carotid n. (lateral branch); 5, internal carotid n. (medial branch); 6, (proximal) stapedial a.; 7, chorda tympani; 8, auricular cartilage; 9, FMTC.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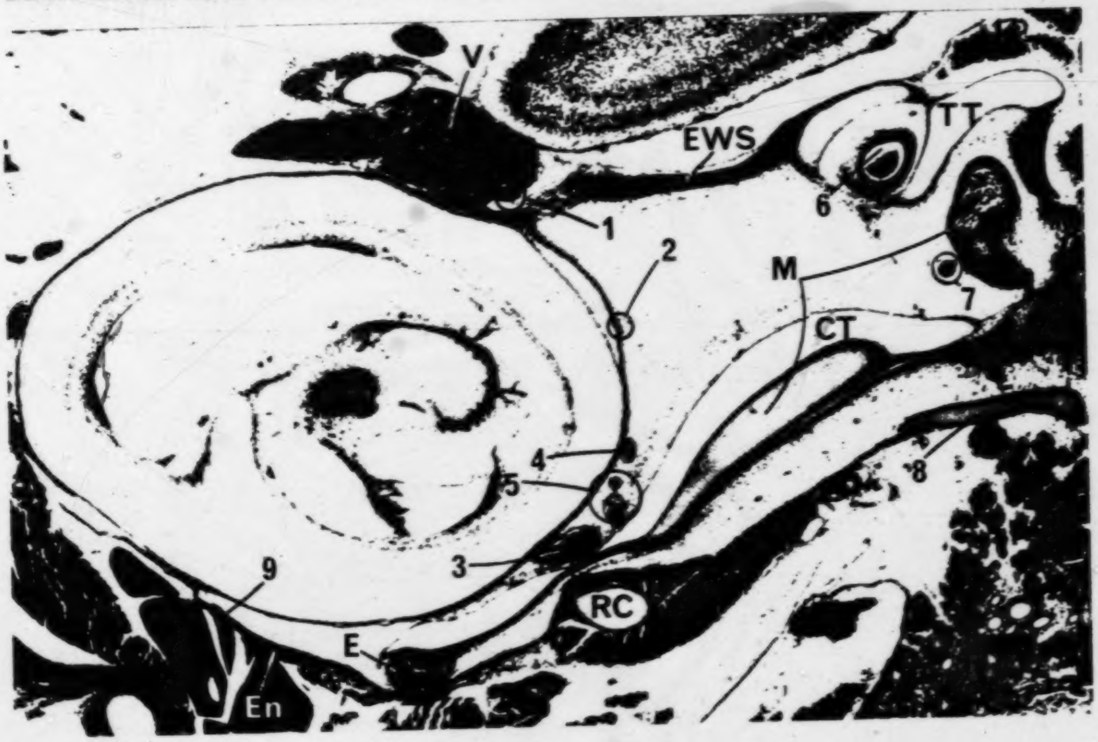
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EWS
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CT
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5
8
3
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RC
E
En

FIG. IV-9 T. glis MPIH 1960/77 (8 days old); s. 1330, cross-section, left side; Azan; x 26.

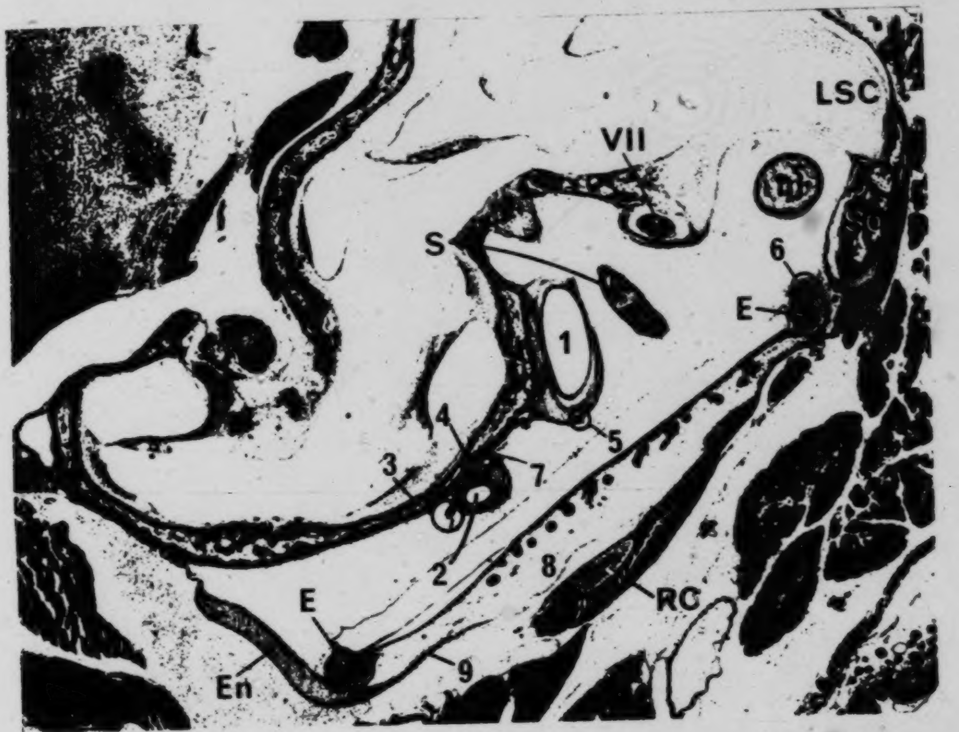
Growth of the entotympanic III. The entotympanic now covers a portion of the ectotympanic, rendering it partially aphaneric (cf. figs. IV-2, IV-13). The cavum tympani is still small; the rest of the presumptive tympanic cavity is filled with mucoid tissue.

1, (proximal), stapedial a.; 2, promontorial a.; 3, internal carotid n. (medial branch); 4, internal carotid n. (lateral branch); 5, tympanic n. (major branch); 6, chorda tympani; 7, inferior tympanic a.; 8, presumptive tissue of membranous meatus; 9, FMTC.

FIG. IV-10 T. glis MPIH 1964/10 (19 days old); s. 1435, cross-section, left side; Azan; x 27.

Growth of the entotympanic IV. The entotympanic forms a complete, cartilaginous ventral wall for the tympanic cavity.

1, (proximal), stapedial a.; 2, promontorial a.; 3, chorda tympani; 4, auricular cartilage; 5, external acoustic meatus.


LSC
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RC
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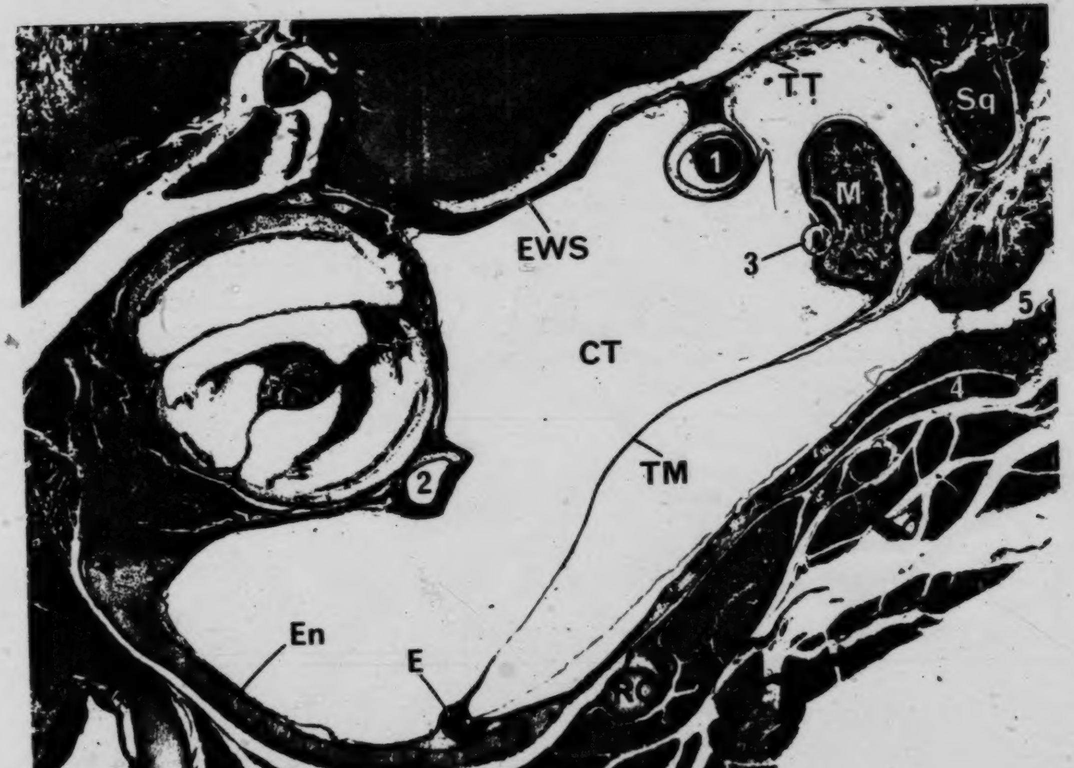
TT
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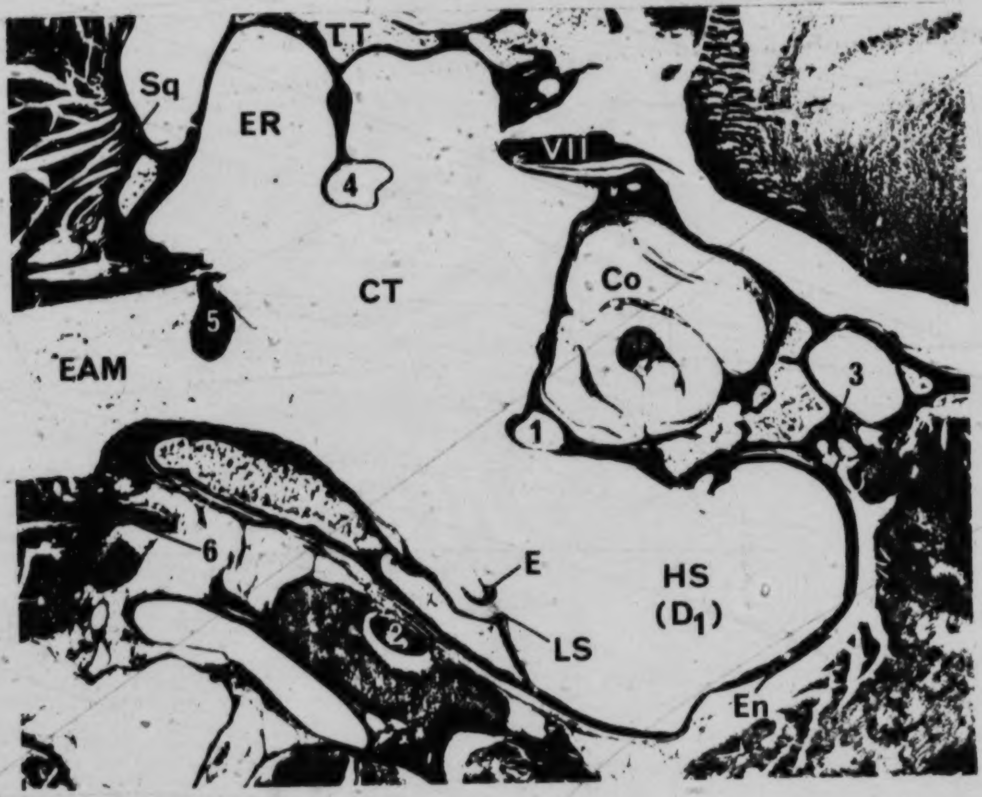
4
TM
2
En
E
Rc

FIG. IV-11 *T. glis* MPIH 1961/11 (adult); s. 2800, cross-section, left side (sides rev.); Azan; x 16.

Growth of the entotympanic V. The definitive, bony bulla forms a shell around the large hypotympanic sinus.

1, promontorial a.; 2, stylohyal; 3, crest on petrosal (?RTPP); 4, (proximal) stapedial a.; 5, malleus (displaced during processing); 6, auricular cartilage.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EAM
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E
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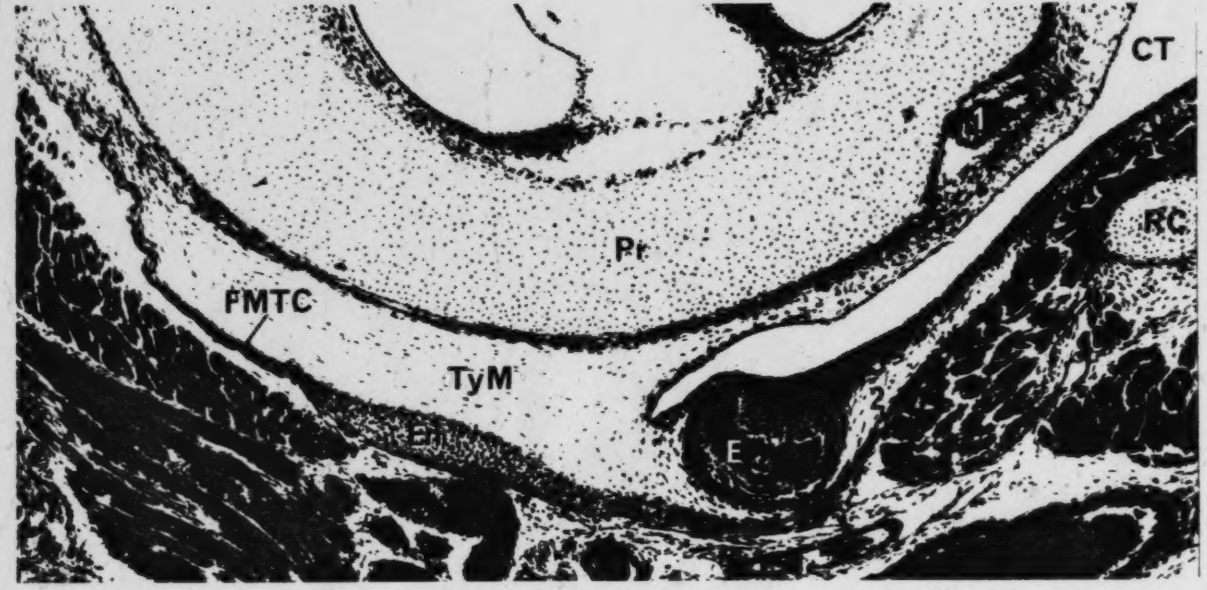
(D1)
2
LS
En

FIG. IV-12 T. glis MPIH 1959/4 (newborn); s. 322/1, cross-section, right side (sides rev.); Azan; x 90.

Relationship of the ectotympanic and entotympanic I. The entotympanic (here represented by its caudal spur) is embedded within the well-developed fibrous membrane of the tympanic cavity, but it has not yet grown around the ectotympanic. Note that the fibrous membrane is not connected to the periosteum of the ectotympanic.

1, promontorial a. and internal carotid n.; 2, presumptive tissues of membranous meatus; 3, tunica mucosa; 4, definitive membranous meatus.


CT
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RC
Pr
FMTC
TyM
2
Em
E

FIG. IV-13 *T. glis* MPIH 1960/77 (8 days old); s. 1330, cross-section, left side; Azan; x 113.

Relationship of the ectotympanic and entotympanic II. This is an enlargement if fig. IV-9. The entotympanic, growing within the fibrous membrane, has passed beneath the ectotympanic. Note the complete absence of sutural tissues.

For key to numbered structures, see fig. IV-12.

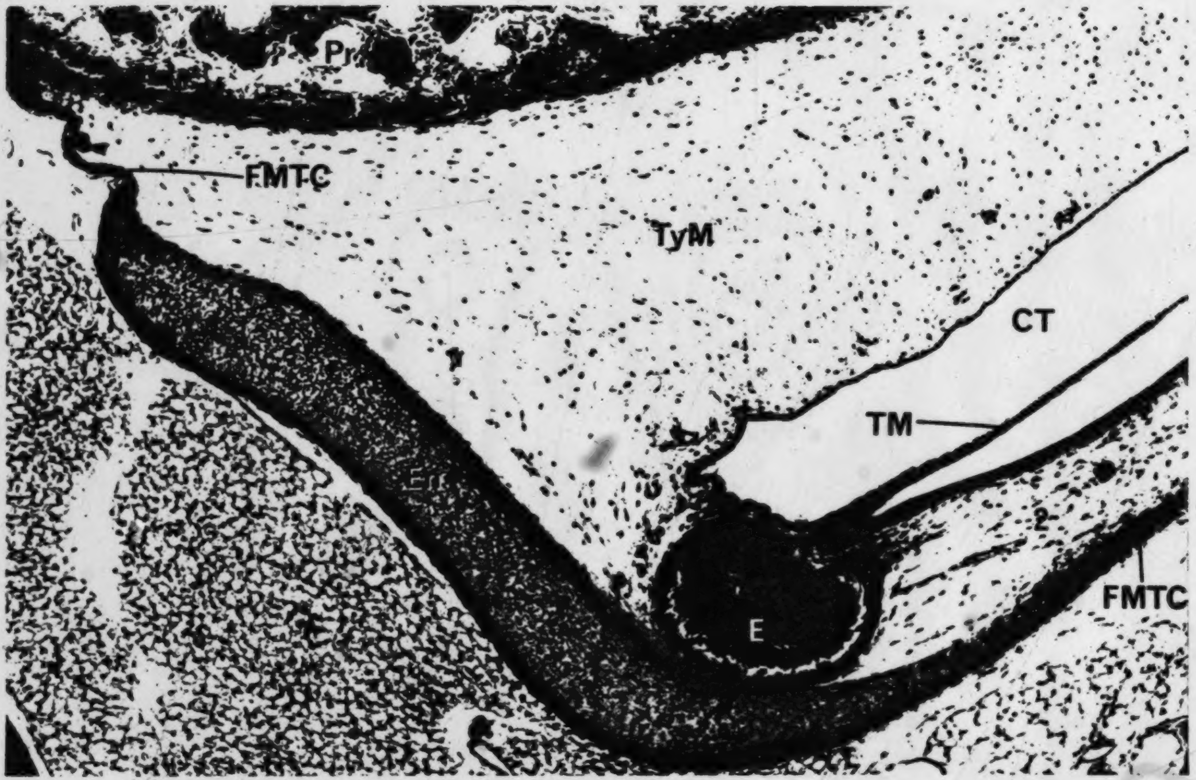

Pr
FMTC
TyM
CT
TM
E
FMTC

FIG. IV-14 T. glis MPIH 1964/10 (19 days old); s. 1505, cross-section, left side; Azan; x 115.

Relationship of the ectotympanic and entotympanic III. The entotympanic continues its laterad expansion within the fibrous membrane. As in previous stages, there is no indication of sutural tissues at the ectotympanic-entotympanic interface. Note also that part of the presumptive tissue of the membranous meatus has become 'intrabullar' along with the ectotympanic.

For key to numbered structures, see fig. IV-12.

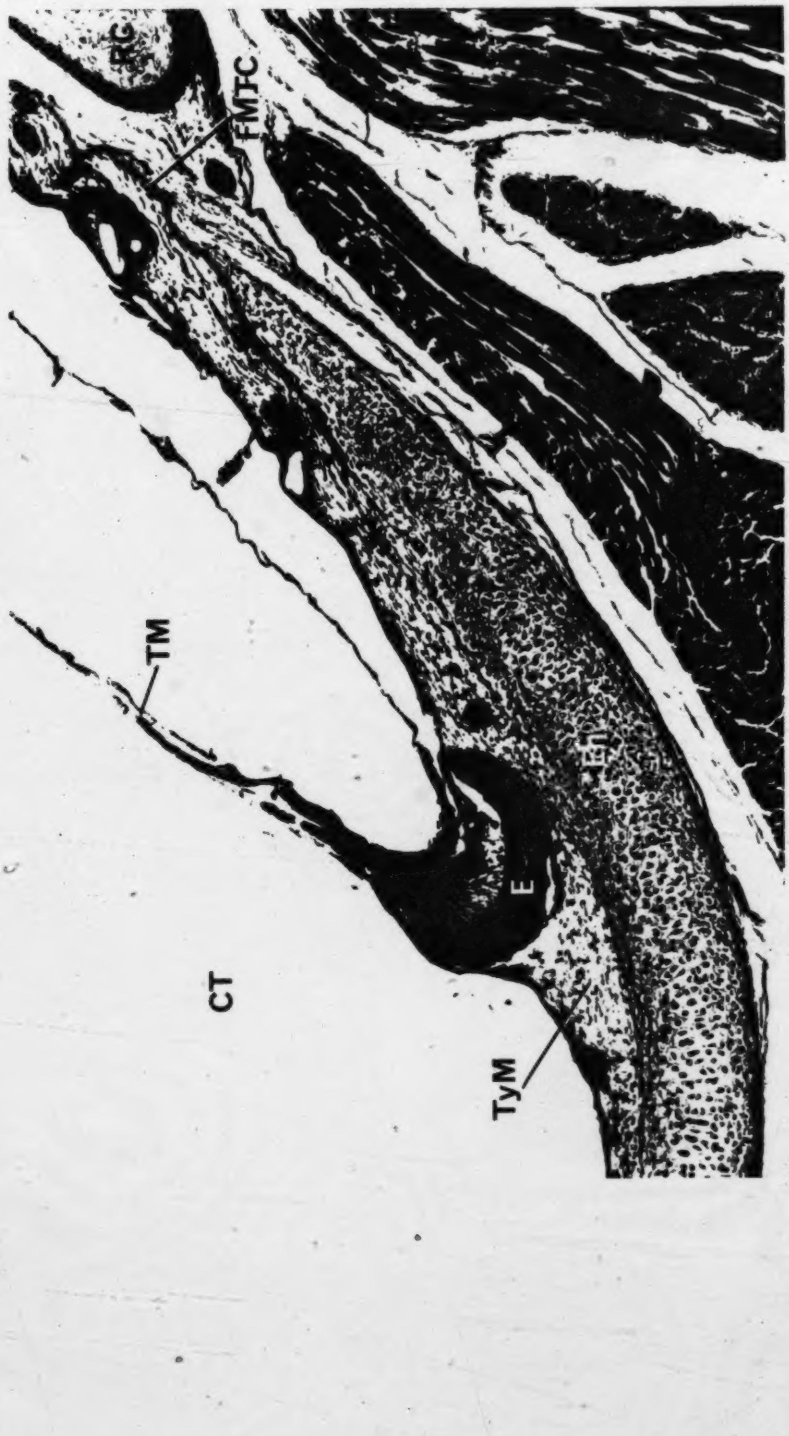
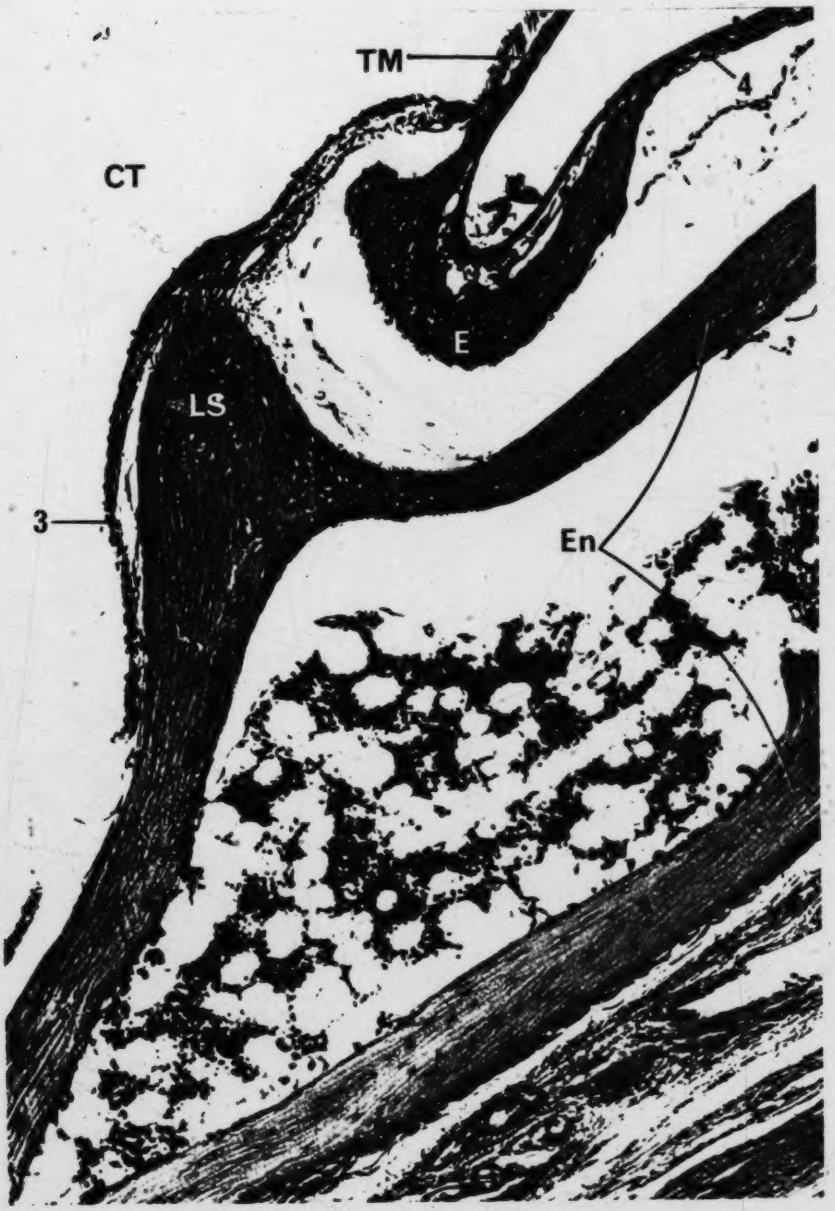

RC
FMTC
TM
El
E
CT
TyM

FIG. IV-15 *T. glis* MPIH 1961/11 (adult); s. 2770, cross-section, left side; Azan; x 175.

Relationship of the ectotympanic and entotympanic IV. Although there is some disruption of soft tissues, it is clear that the ectotympanic is connected to the bullar wall by means of the tissues of the tunica mucosa and the membranous meatus. No independent 'anulus membrane' or true sutural tissues are in evidence.

For key to numbered structures, see fig. IV-12.


TM
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CT
E
LS
3
En

FIG. IV-16 T. glis MPIH 1960/82a (near-term fetus); s. 940, cross-section, right side (sides rev.); Azan; x 32.

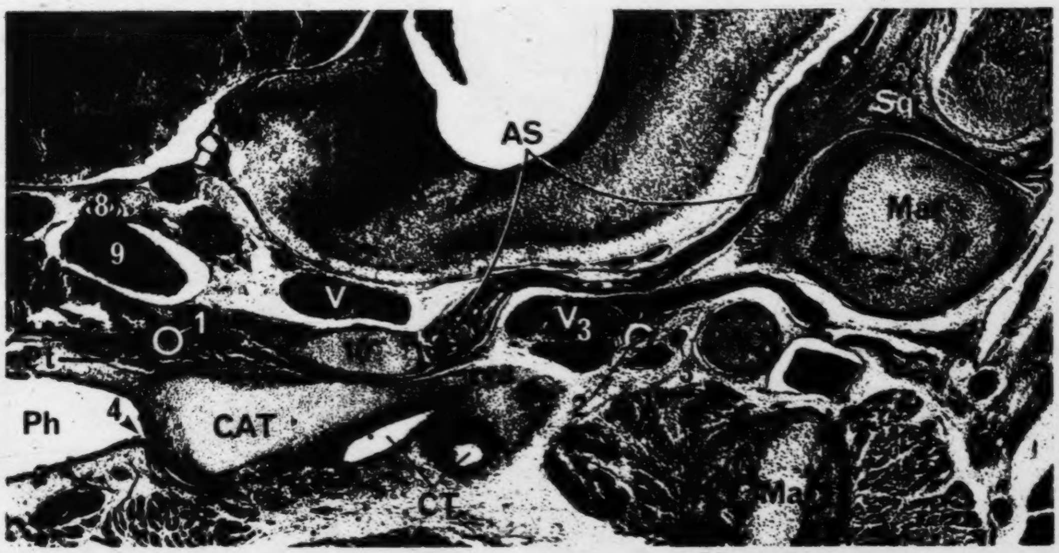
Section through pharyngeal end of auditory tube. Comparisons with adult conditions (cf. fig. IV-38a,b) suggests that the rostral part of the homogeneous anterior mass of cartilage eventually becomes the (true) cartilage of the auditory tube. However, at this stage there is no histological difference between this section and the rest of the anterior mass (cf. figs. IV-17, IV-18).

For key to numbered structures, see fig. IV-17.

FIG. IV-17 T. glis MPIH 1960/82a (near-term fetus); s. 960, cross-section, right side (sides rev.); Azan; x 32.

Anterior end of presumptive tympanic cavity. This section reveals the complicated shape of the anterior mass of cartilage immediately posterior to the level of the auditory tube (cf. fig. IV-16). On morphological grounds, this section of the anterior mass is probably composed of entotympanic material alone. It contains the rostral end of the medial diverticulum (D_2) of the hypotympanic sinus and the anterior septum, both of which are enclosed or formed by the entotympanic in the adult (fig. IV-3).

1, nerves of the pterygoid canal; 2, ramus inferior of the stapedial a.; 3, chorda tympani, 4, auditory tube; 5, diverticulum D_2; 6, lesser petrosal n.; 7, anterior septum; 8, promontorial a. (cerebral carotid a.) within cranial cavity; 9, cavernous sinus; 10, ala temporalis.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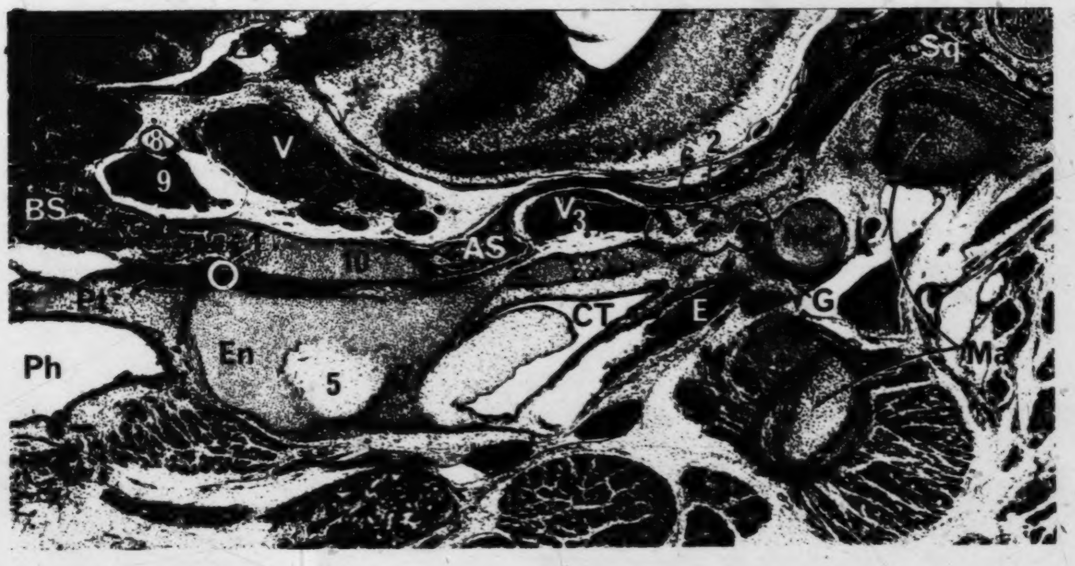
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FIG. IV-18 T. glis MPIH 1960/82a (near-term fetus); x. 1000, cross-section, right side (sides rev.); Azan; x 32.

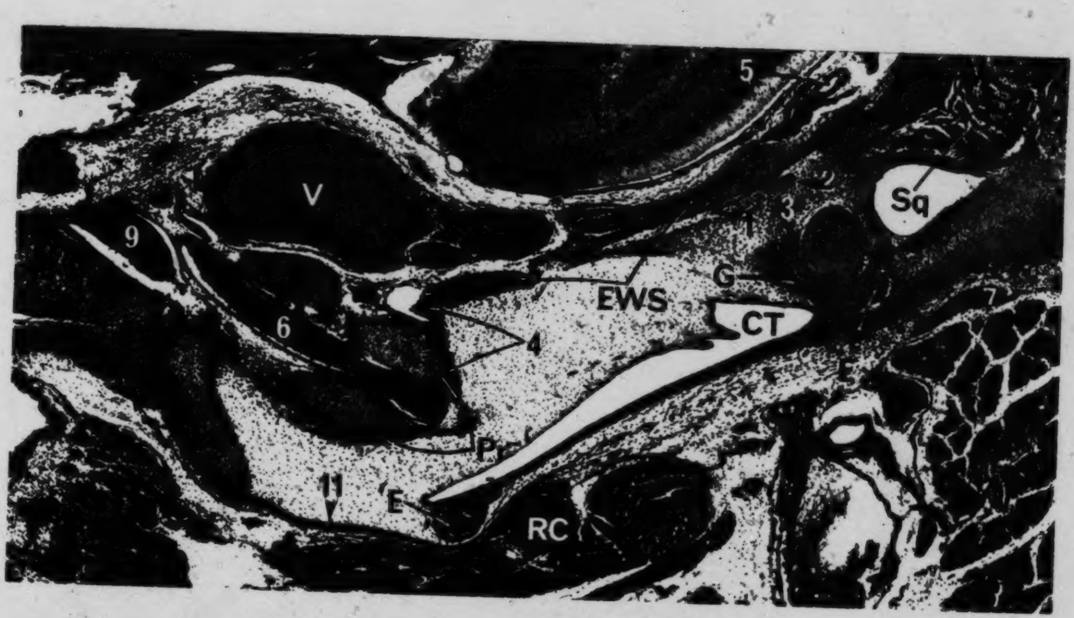
Section through foramen caroticum primitivum and anterior pole of promontory. The entotympanic continues a short distance further in the medioventral wall of the presumptive tympanic cavity.

For key to numbered structures, see fig. IV-19.

FIG. IV-19 T. glis MPIH 1960/82a (near-term fetus); s. 1010, cross-section, right side (sides rev.); Azan; x 32.

Terminal part of the entotympanic. The entotympanic ends within the fibrous membrane of the tympanic cavity immediately posterior to the level of the anterior pole of the promontory at this stage.

1, lesser petrosal n.; 2, ramus inferior of stapedial a.; 3, chorda tympani; 4, deep and greater petrosal nn. (nerves of the pterygoid canal); 5, ramus superior of the stapedial a. (middle meningeal a.); 6, promontorial a.; 7, auricular cartilage; 8, alicochlear commissure; 9, cavernous sinus; 10, basioccipital-basisphenoidal synchondrosis; 11, FMTC.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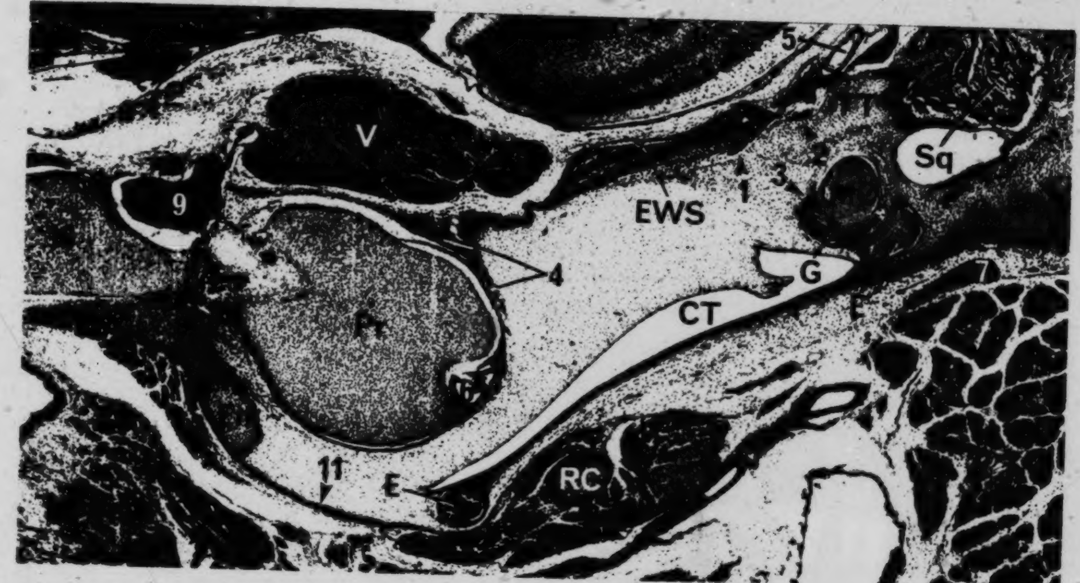
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FIG. IV-20 *T. glis* MPIH 1960/82a (near-term fetus); s. 1120, cross-section, right side (sides rev.); Azan; x 32.

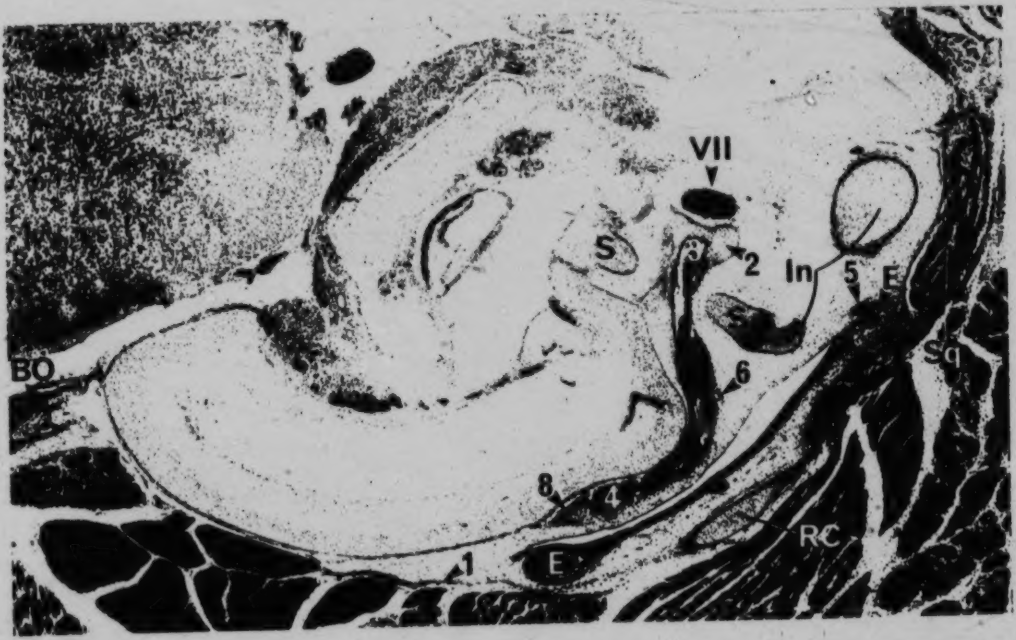
Bifurcation of the internal carotid cartery into promontorial and (proximal) stapedial branches. The cartilage of the tegmen tympani migrates along the stapedial artery, eventually forming a complete canal around the vessel.

For key to numbered structures, see fig. IV-21.

FIG. IV-21 *T. glis* MPIH 1960/82a (near-term fetus); s. 1140, cross-section, right side (sides rev.); Azan; x 32.

Entry of the internal carotid artery and nerve into the middle ear. The processes recessus does not contribute, or only very little, to the bulla (cf. lorises and lemurs, figs. II-1, III-1). The anterior end of the caudal tympanic process of the petrosal (12) is confluent with the medial wall of the facial sulcus.

1. FMTC; 2, cartilage of the stapedial canal; 3, (proximal) stapedial artery; 4, promontorial a.; 5, chorda tympani; 6, tympanic nerve (major branch); 7, stapedius m.; 8, internal carotid n.; 9, internal carotid a.; 10, perilymphatic duct; 11, secondary tympanic membrane; 12, anterior end of CTPP.


VII
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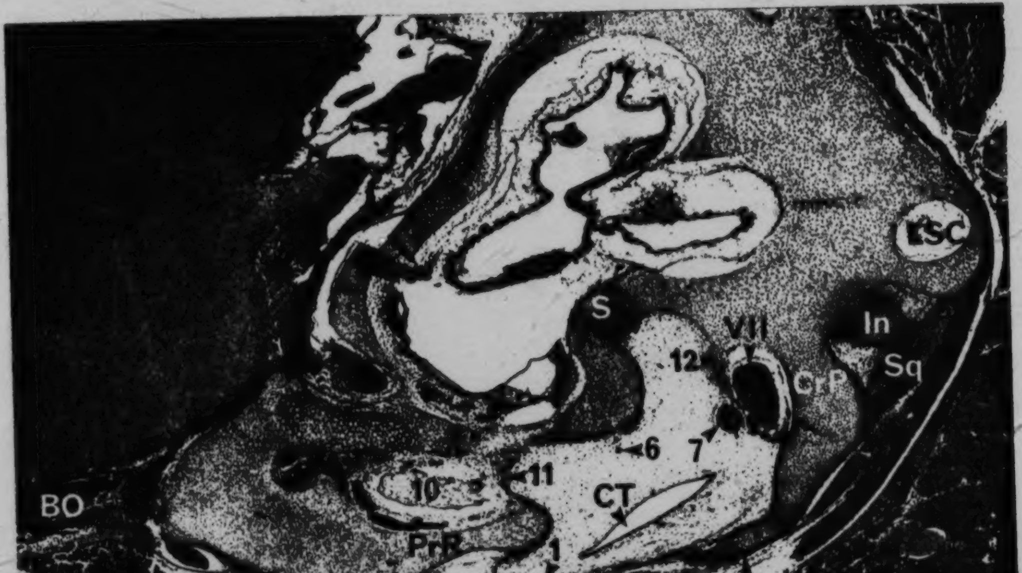
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FIG. IV-22 T. glis MPIH 1960/82a (near-term fetus); s. 1160, cross-section, left side; Azan; x 46.

Middle part of the caudal tympanic process of the petrosal. The process forms, with the posterior continuation of the crista parotica, a deep fossa for the stapedius muscle.

1, stapedius m.; 2, tympanic n. (major branch); 3, posterior continuation of the crista parotica beneath the prominence of the lateral semicircular canal; 4, FMTC; 5, auricular ramus of the vagus n.; 6, part of the facial n.

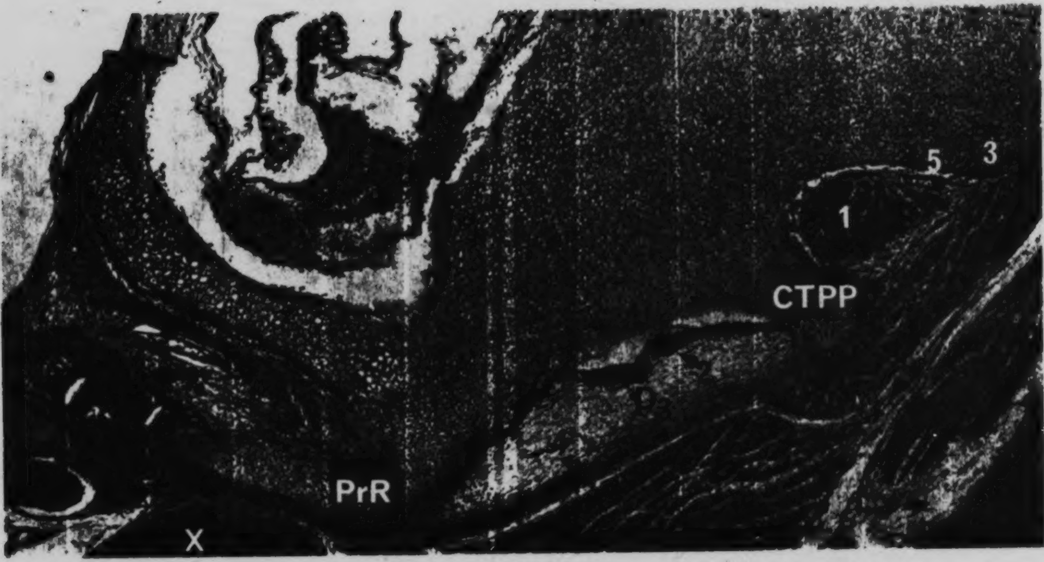
FIG. IV-23 T. glis MPIH 1960/82a (near-term fetus); s. 1170, cross-section, left side; Azan; x 56.

Posterior part of the caudal tympanic process of the petrosal. In lemurs and lorises (cf. figs. II-16, III-19), the posterior continuation of the crista parotica is incorporated into the lateral part of the CTPP. In tree shrews, the lateral part of the CTPP forms medial to the stapedius muscle, and the posterior continuation of the crista parotica does not take part in the construction of the bulla.

For key to numbered structures, see fig. IV-22.

FIG. IV-24 T. glis MPIH 1959/4 (newborn); s. 304/1, cross-section, left side; Azan; x 22.

Anterior end of presumptive tympanic cavity (cf. fig. IV-17).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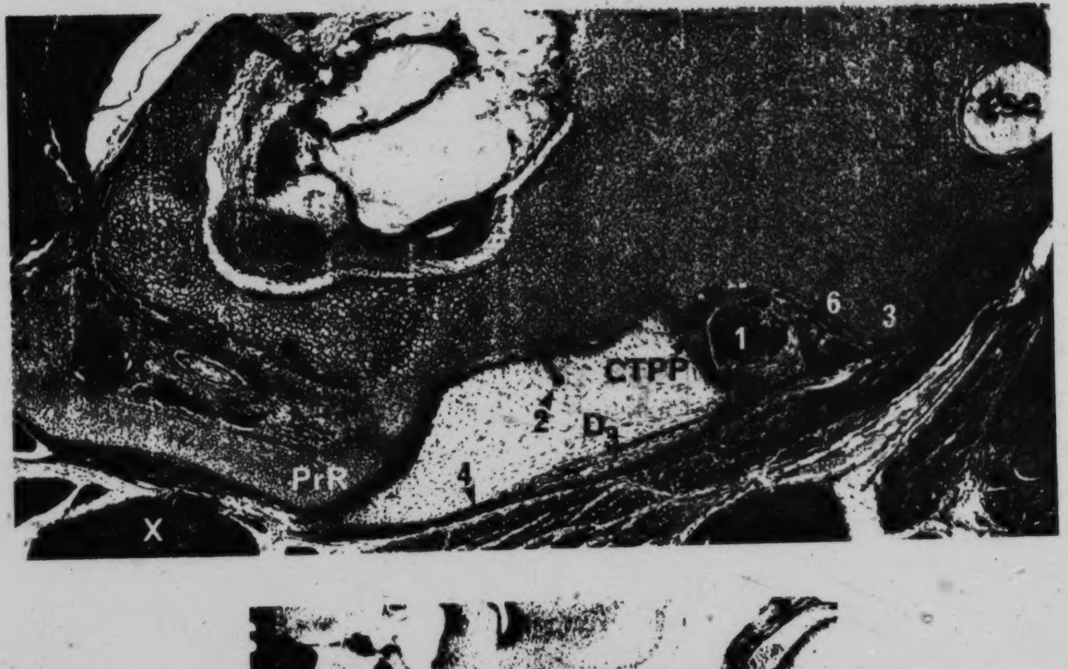
PrR
X


6
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CTPP
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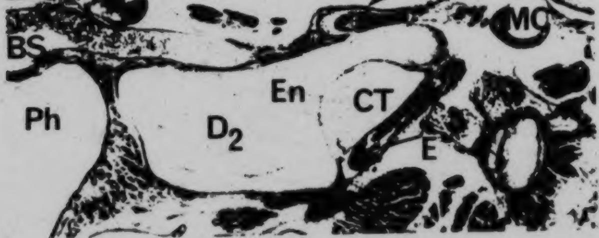
D_3
PrR
4
X


AS
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Ph
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CT
D_2
E

FIG. IV-25 T. glis MPIH 1959/4 (newborn); s. 345/2, cross-section, right side; Azan; x 33.

Middle of the presumptive tympanic cavity. Note small size of epitympanic recess (containing incudomalleolar joint) and the complete, cartilaginous canal for the (proximal) stapedial artery.

1, (proximal) stapedial a.; 2, chorda tympani; 3, internal carotid n.; 4, promontorial a.; 5, tympanic nerve (major branch); 6, FMTC; 7, suprafacial commissure.

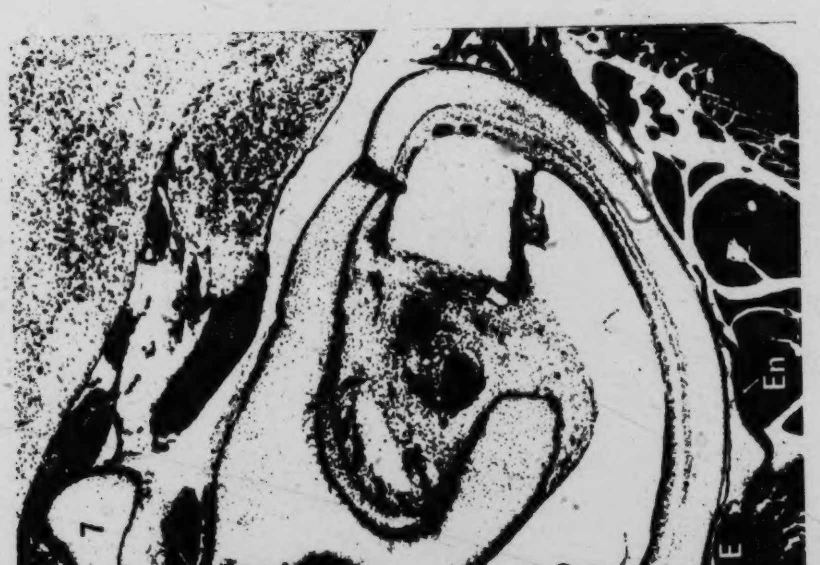
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FIG. IV-26 *T. glis* MPIH 1959/4 (newborn); s. 360/4, cross-section, right side (sides rev.); Azan; x 30.

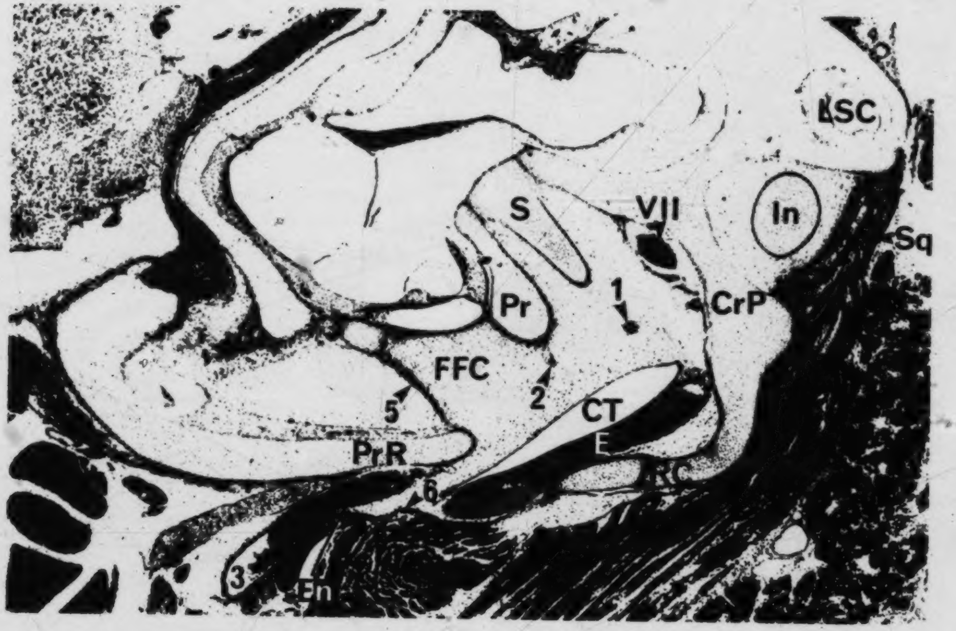
Terminal part of entotympanic. The caudal spur ends at the level of the posterior carotid foramen at this stage (cf. fig. IV-1).

1, tendon of stapedius m.; 2, tympanic nerve (major branch); 3, internal carotid a.; 4, internal carotid n.; 5, secondary tympanic membrane; 6, FMTC.

FIG. IV-27 *T. glis* MPIH 1959/4 (newborn); s. 378/4, cross-section, left side; Azan; x 41.

Posterior part of caudal tympanic process of the petrosal (cf. fig. IV-24).

1, stapedius m. in stapedius fossa; 2, tympanic n. (major branch) entering D_3 through FMTC; 3, FMTC; 4, auricular ramus of vagus n.; 5, posterior continuation of crista parotica.


LSC
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FFC
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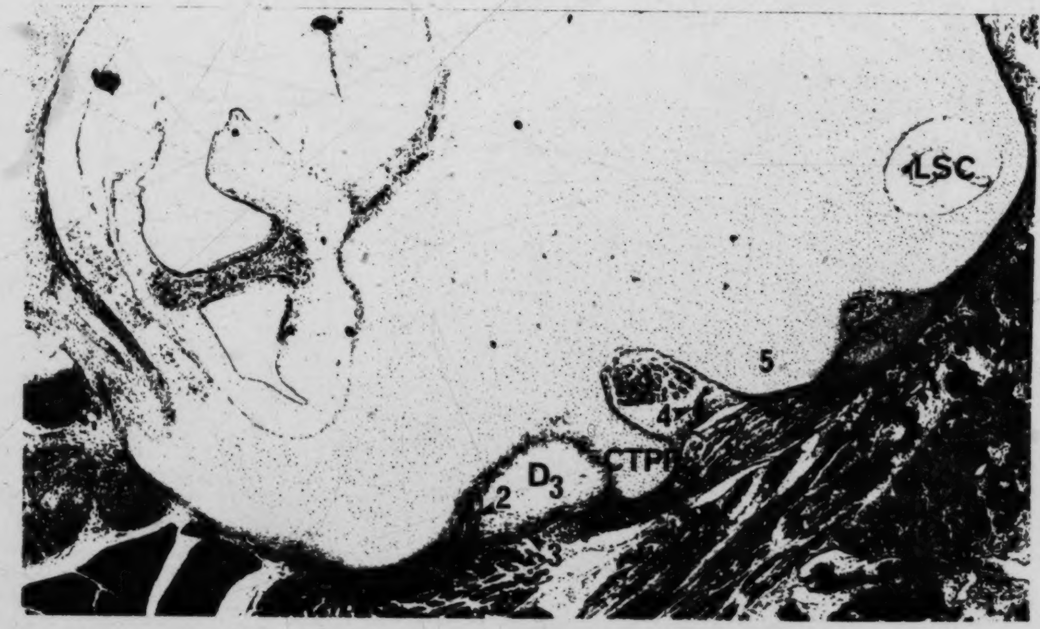

LSC
5
4
D3
CTPr
2
3

FIG. IV-28 *T. glis* MPIH 1960/77 (8 days old); s. 1145, cross-section, left side; Azan; x 30.

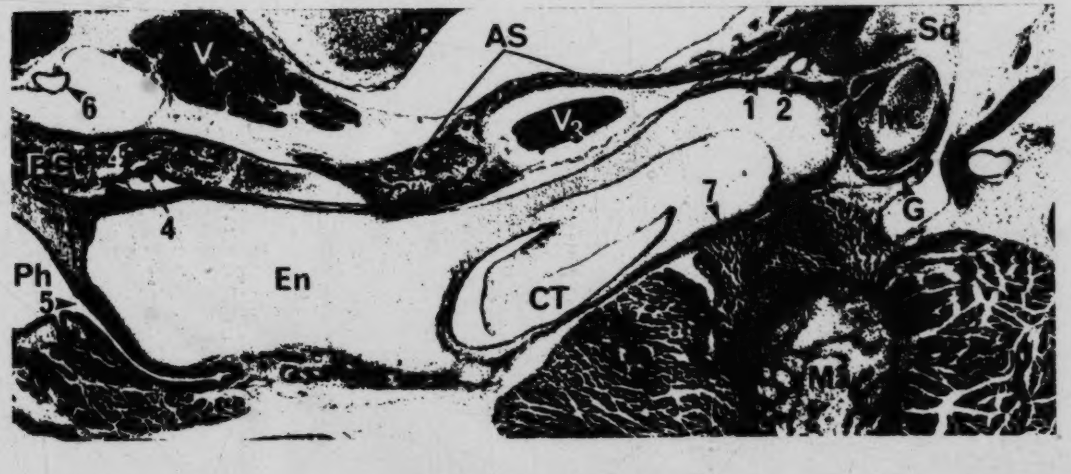
There is still no histological difference between the material of the entotympanic and that of the cartilage of the auditory tube. In this section, the material immediately adjacent to the auditory tube probably remains cartilaginous (i.e., becomes the definitive cartilage of the tube). The rest may be regarded as the entotympanic (cf. figs. IV-32, IV-38a,b).

1, lesser petrosal n.; 2, ramus inferior of the stapedial a.; 3, chorda tympani; 4, nerves of the pterygoid canal; 5, auditory tube (lumen); 6, promontorial a. (cerebral carotid a.); 7, FMTC.

FIG. IV-29 *T. glis* MPIH 1960/77 (8 days old); s. 1190, cross-section right side (sides rev.); Azan; x 31.

The complicated relationships of septa and diverticula in the anterior part of the tympanic cavity are well displayed in this young postnatal specimen. The entotympanic and anterior end of the tegmen tympani are fused by means of a commissure (see fig. IV-2).

1, promontorial a. (cerebral carotid a.); 2, alicochlear commissure; 3, nerves of the pterygoid canal; 4, lesser petrosal nerve in its canal; 5, ramus superior of the stapedial a.; 6, entotympanic-tegminal commissure; 7, chorda tympani; 8, innominate diverticulum; 9, lateral secondary septum.


AS
Sq
V
6
V3
1
2
3
MC
BS
4
4
7
G
Ph
5
En
CT
M

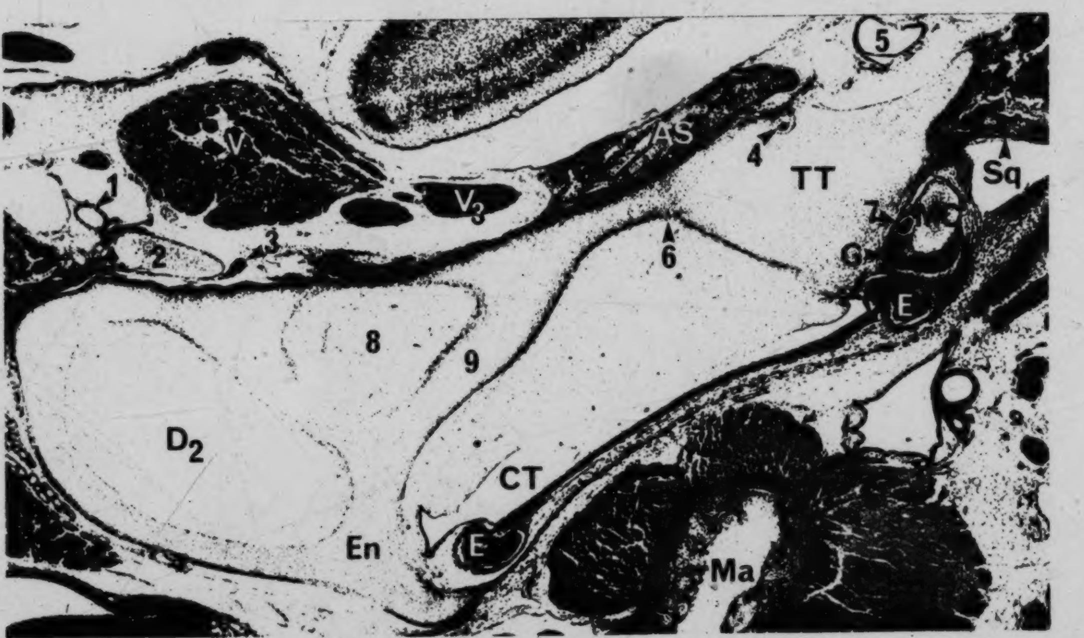

5
AS
4
TT
Sq
V
1
V3
7
MC
2
3
6
G
E
8
9
D2
CT
En
E
Ma

FIG. IV-30 T. glis MPIH 1960/77 (8 days old); s. 1215, cross-section, left side; Azan; x 28.

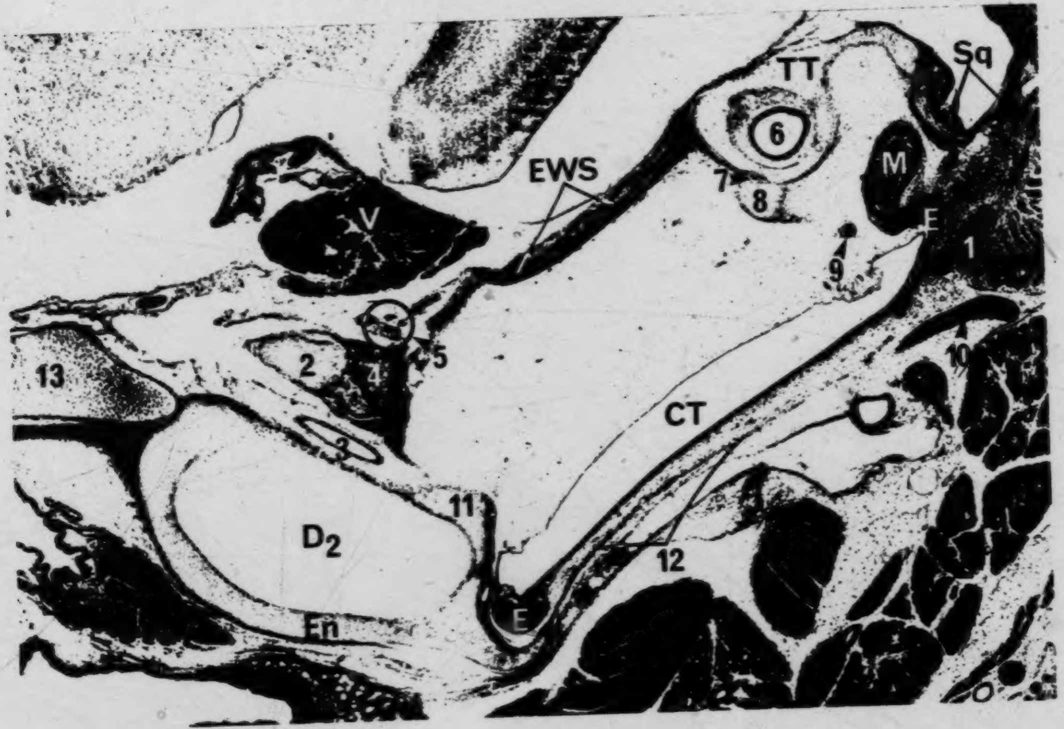
The anterior septum has reached the anterior pole of the promontory by this stage and forms part of the eventual canal for the promontorial artery. The alicochlear commissure is in the process of degeneration. Also illustrated is the extreme posterior end of the entotympanic-tegminal commissure; note that the fusion of the two structures is not complete in this region.

1, lumen of the external acoustic meatus; 2, alicochlear commissure; 3, promontorial a.; 4, anterior pole of the promontory; 5, nerves of the pterygoid canal; 6, (proximal) stapedial a.; 7, lesser petrosal n.; 8, extreme posterior end of entotympanic-tegminal commissure; 9, chorda tympani; 10, auricular cartilage; 11, anterior septum; 12, FMTC; 13, basioccipital-basisphenoidal synchondrosis.

FIG. IV-31 T. glis MPIH 1960/77 (8 days old); s. 1410, cross-section, left side; Azan; x 36.

The entotympanic also fuses with the caudal tympanic process of the petrosal.

1, internal carotid n.; 2, internal carotid a.; 3, tympanic n. (communicating branch); 4, tympanic n. (major branch); 5, entotympanic-CTPP commissure; 6, stapedius m. in stapedius fossa.


TT
Sq
6
EWS
7
8
M
V
E
9
1
5
2
4
13
10
CT
3
11
D2
12
En
E

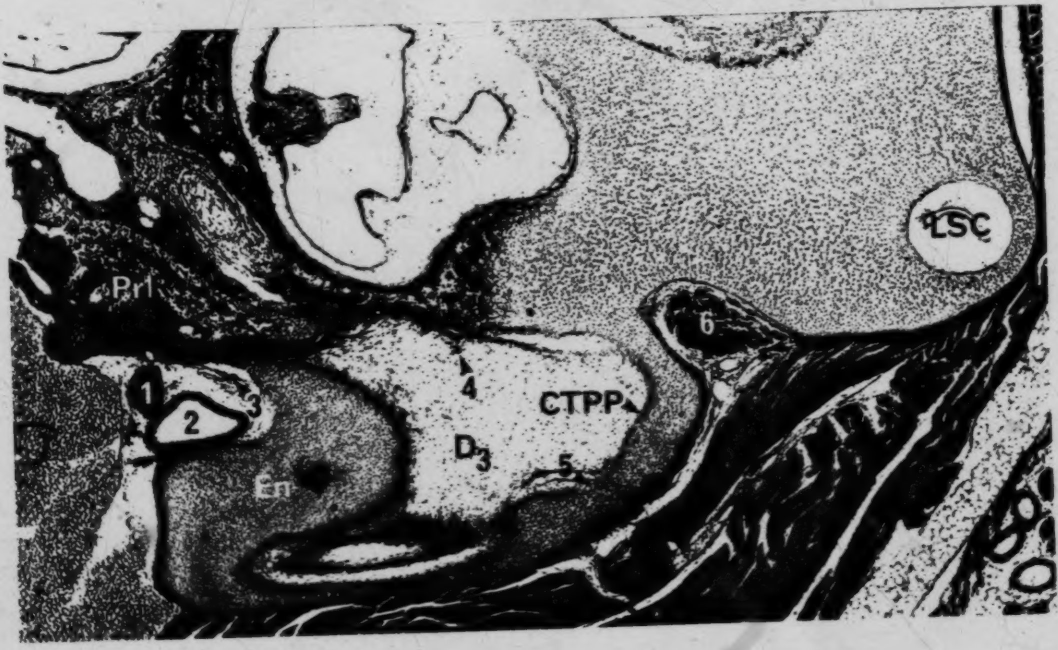

LSC
Pr1
6
4
1
2
3
CTPP
D3
5
En

FIG. IV-32 T. glis MPIH 1964/10 (19 days old); s. 1270, cross-section, left side; Azan; x 43.

It is still not clear, even at this late stage, how much of the anterior mass of cartilage becomes true tubal cartilage. However, at least an incipient division is now indicated: included in this section is the rostralmost extent of the ossification center of the entotympanic (see also figs. IV-33, IV-34). Bony areas are indicated by asterisks.

FIG. IV-33 T. glis MPIH 1964/10 (19 days old); s. 1300, cross-section, right side; Azan; x 17.

The anterior parts of the entotympanic are now extensively ossified.

1, nerves of the pterygoid canal; 2, promontorial a. (cerebral carotid a.); 3, chorda tympani; 4, anterior septum.

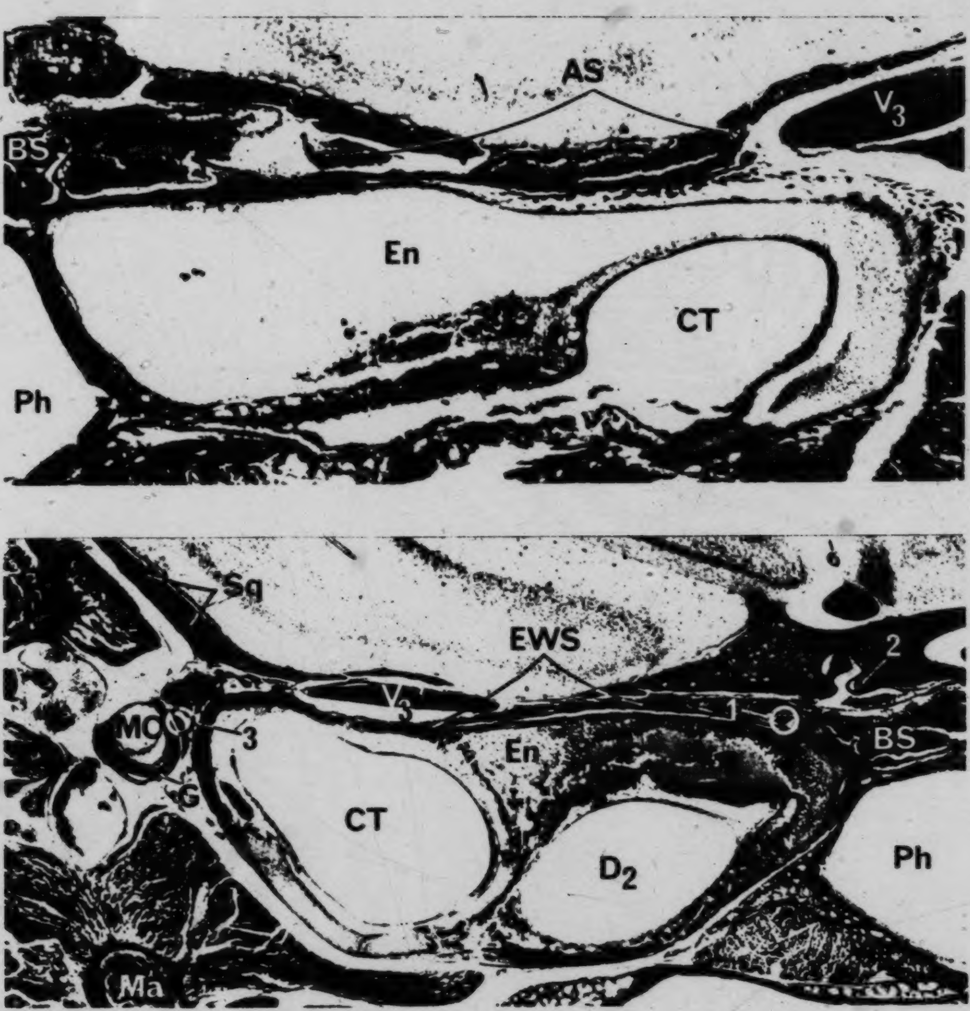

AS
V$_3$
BS
En
CT
Ph
Sq
EWS
2
V$_3$
1
MC
3
BS
En
G
CT
D$_2$
Ph
Ma

FIG. IV-34 T. glis MPIH 1964/10 (19 days old); s. 1375, cross-section, left side (sides rev.); Azan; x 17.

The entotympanic is highly ossified in the area of the anterior septum, which suggests that its center first appears near this feature. Although it is not evident in this figure because of the low degree of magnification, the dorsal part of the entotympanic extends beneath the epitympanic wing of the sphenoid, hiding it from the ventral.

1, ramus superior of the stapedial a. (as middle meningeal a.); 2, promontorial a. entering cranial cavity; 3, nerves of the pterygoid canal; 4, anterior septum; 5, auricular cartilage; 6, basioccipital-basisphenoidal synchondrosis.

FIG. IV-35 T. glis MPIH 1964/10 (19 days old); s. 1570, cross-section, right side (sides rev.); Azan; x 17.

There is never a close association between the entotympanic and Reichert's cartilage during the former's growing phase (see also fig. IV-41). The two abut one another, but are not fused. A small part of the auditory capsule is still exposed between the medial margin of the entotympanic and the basioccipital.

1, cranial cervical ganglion of the autonomic nervous system; 2, internal carotid n.; 3, internal carotid a.; 4, stapedius m.; 5, secondary tympanic membrane; 6, incus; 7, tympanic n. (communicating branch); 8, tympanic n. (major branch).

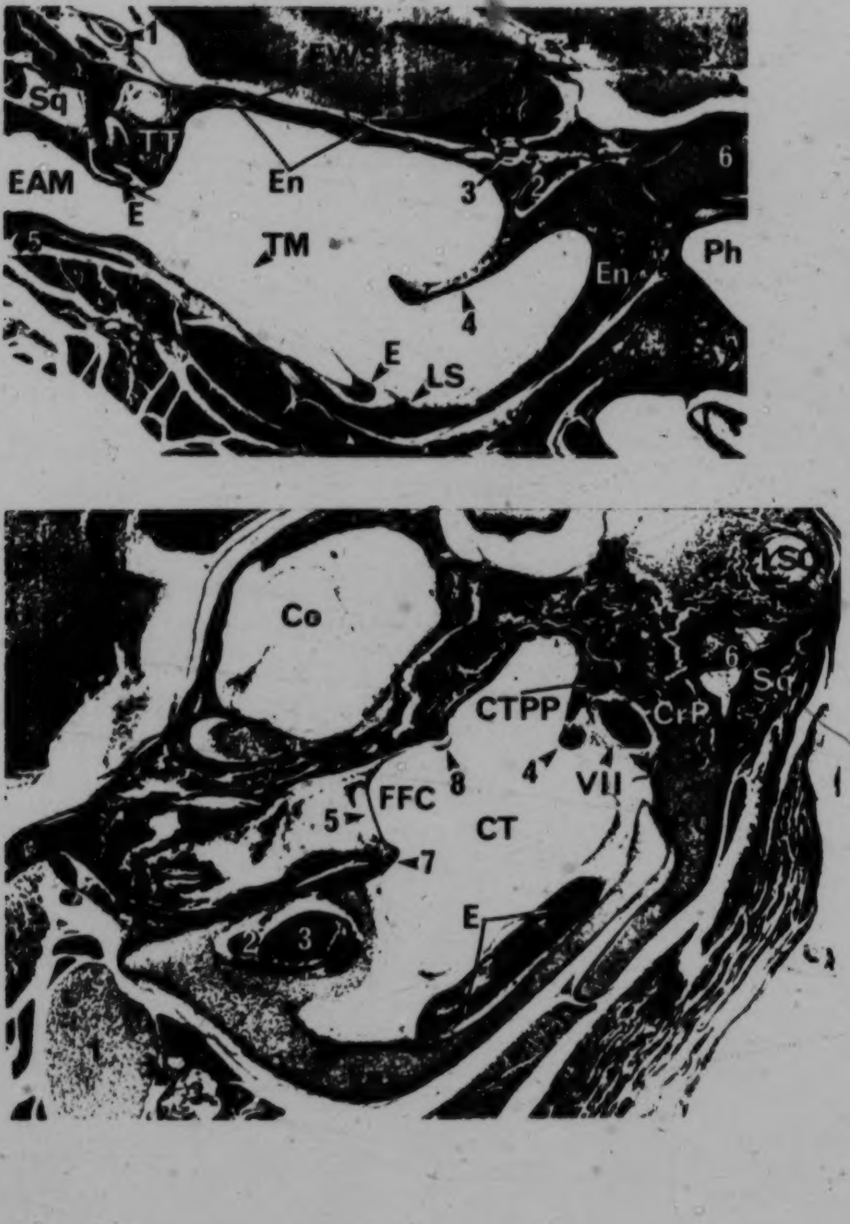

1
Sq
TT
EAM
E
En
TM
3
2
6
Ph
En
4
5
E
LS
Co
LSC
6
Sq
CTPP
CrP
4
VII
8
FFC
5
CT
7
E
2
3
1

FIG. IV-36 *T glis* MPIH 1964/10 (19 days old); s. 1605, cross-section, left side; Azan; x 50.

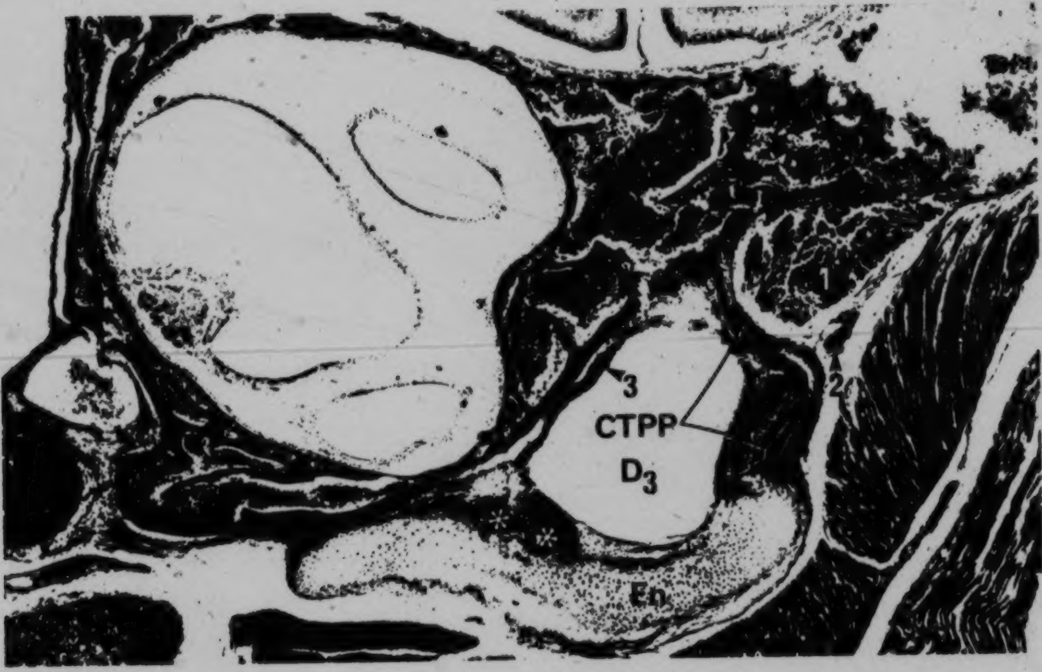
The posterior part of the entotympanic is still cartilaginous, although the caudal tympanic process of the petrosal is fully ossified. In this section, trabeculae of the petrosal seem to extend into the substance of the entotympanic. The area indicated by asterisks consists of bone derived from the caudal tympanic process of the petrosal, not from the entotympanic center further forwards.

1, stapedius m. in stapedius fossa; 2, auricular ramus of the vagus; 3, tympanic n. (major branch).

FIG. IV-37 *T. glis* MPIH 1964/10 (19 days old); s. 1615, cross-section, right side (sides rev.); Azan; x 50.

In this section, the caudal tympanic process of the petrosal is clearly separated from the still-cartilaginous part of the entotympanic by a zone of fibres. The major branch of the tympanic nerve enters diverticulum D_3 through a foramen in the extreme posterior end of the bulla, between the entotympanic and the CTPP (cf. figs. IV-5, IV-27).

For key to numbered structures, see fig. IV-36.


1
2
3
CTPP
D_3
En

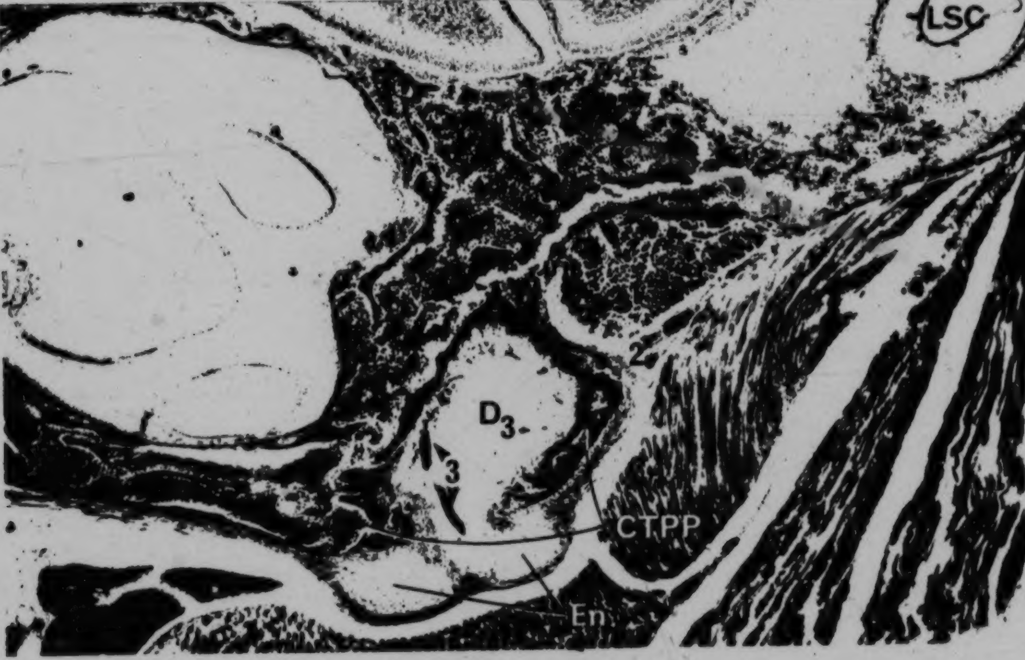

LSC
2
D_3
3
CTPP
En

FIG. IV-38 T. glis MPIH 1961/11 (adult).

a. s. 2530, cross-section, left side; Azan; x 15. The cartilage of the auditory tube is quite small in the adult, and does not extend posteriorly beyond the level of the tympanic aperture of the tubal canal.

b. same section, enlargement of area in box in fig. IV-38a; x 120. There is no zone of intergradation between the cartilage of the tube and the bone of the entotympanic; the two are separated by dense connective tissues representing their combined perichondrium and periosteum (arrows). This condition implies that there is a real difference between tubal and entotympanic material, even if this cannot be detected histologically in earlier stages.

1, promontorial a. (cerebral carotid a.); 2, nerves of the pterygoid canal; 3, pharyngeal aperture of the auditory tube; 4, tympanic aperture of the auditory tube.

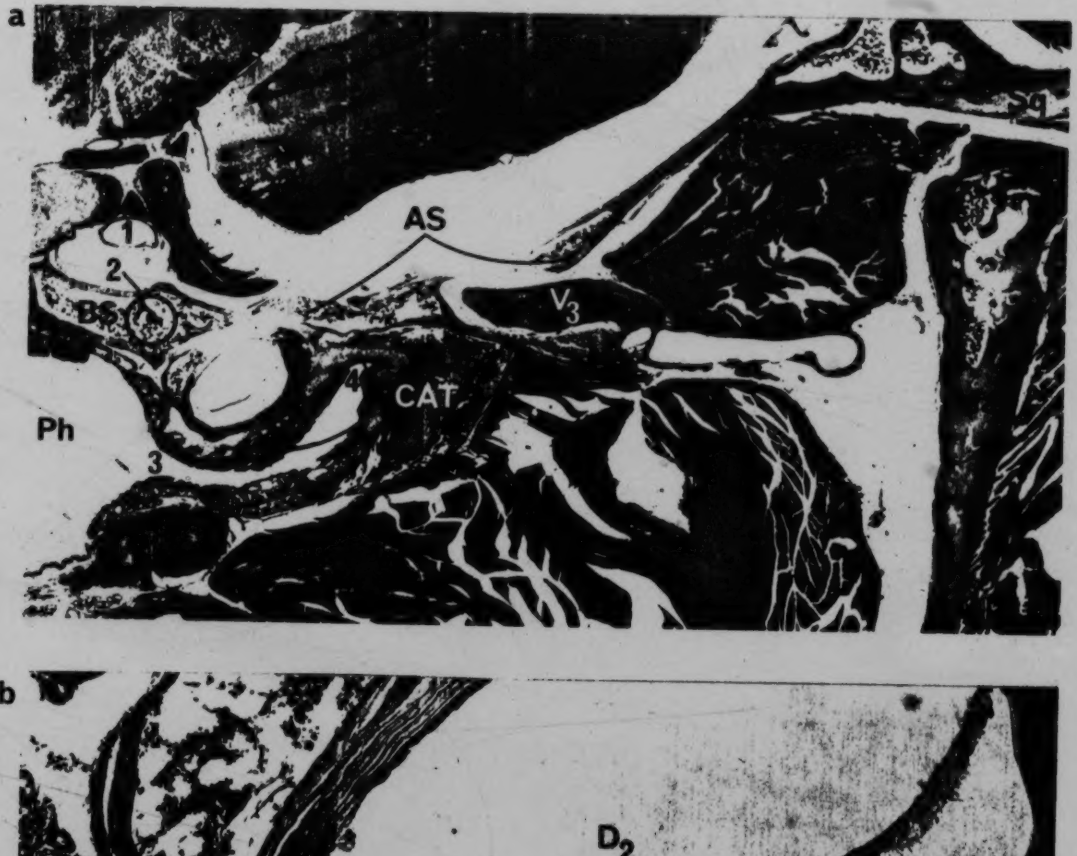

a
AS
1
2
BS
Ph
3
CAT
V_3
b
D_2
En
CAT
AT

FIG. IV-39 T. glis MPIH 1961/11 (adult).

a. s. 2750, cross-section, left side; Azan; x 46. Anterior end of the bulla, showing relationship between ectotympanic, lateral bullar wall, and surrounding soft tissues.

b. s. 2740, cross-section, left side; Azan; x 90. Detail of ventral rim of the external acoustic meatus, showing nodules of cartilage-like material on its lip (asterisks).

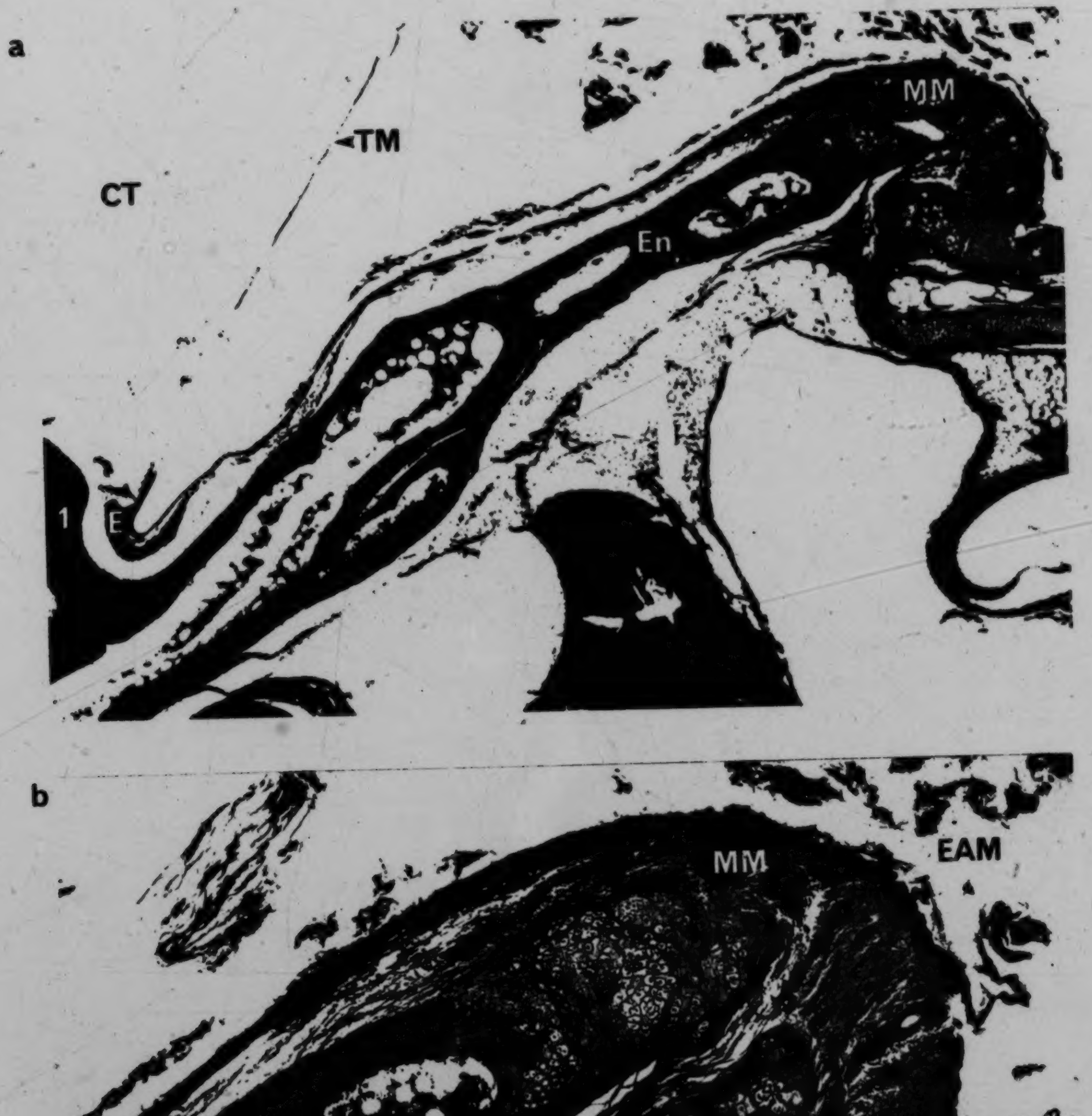

a
CT
TM
MM
En
1
E
b
MM
EAM
En

FIG. IV-40 *T. glis* MPIH 1961/11 (adult); s. 2920, cross-section, left side; Azan; x 19.

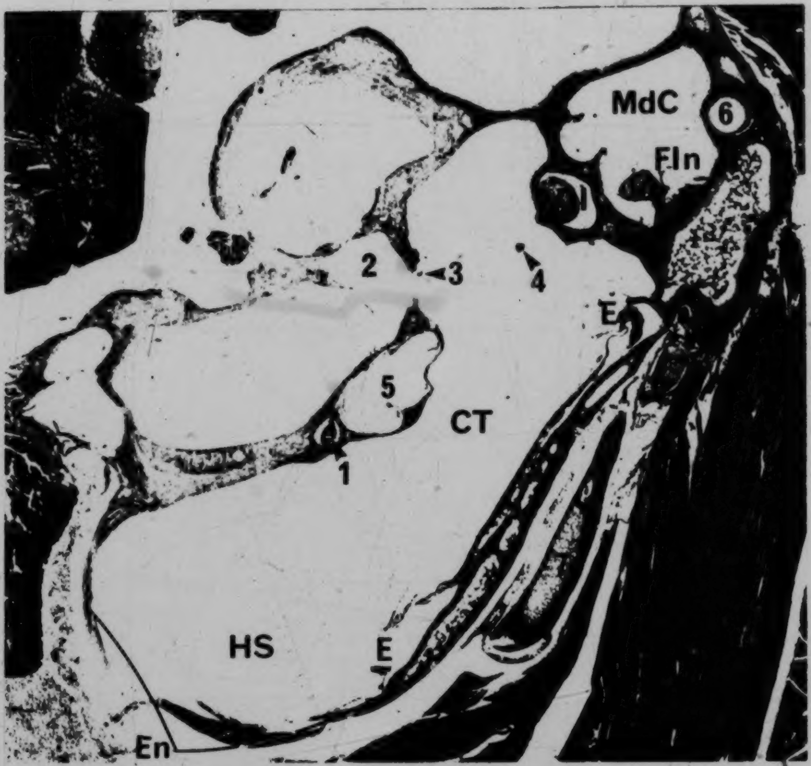
Posterior end of tympanic cavity, showing small mastoid cavity above fossa incudis. Note also the small size of the branches of the tympanic nerve compared to the internal carotid nerve.

1, internal carotid n.; 2, fossula fenestrae cochleae; 3, tympanic nerve (major branch); 4, tendon of stapedius m. in pyramidal canal; 5, carotid canal (artery disrupted during processing); 6, lateral semicircular canal.

FIG. IV-41 *T. glis* MPIH 1961/11 (adult); s. 2940, cross-section, left side; Azan; x 33.

Posterior end of tympanic cavity, showing end of small mastoid cavity. The tympano-styloid cartilage is an unossified remnant of Reichert's cartilage.

1, internal carotid n.; 2, tympanic n. (communicating branch); 3, tympanic n. (major branch); 4, stapedius m. in pyramidal canal; 5, carotid canal; 6, lateral semicircular canal; 7, tympano-styloid cartilage; 8, secondary tympanic membrane.


MdC
6
Fln
2
3
4
E
5
CT
1
HS
E
En

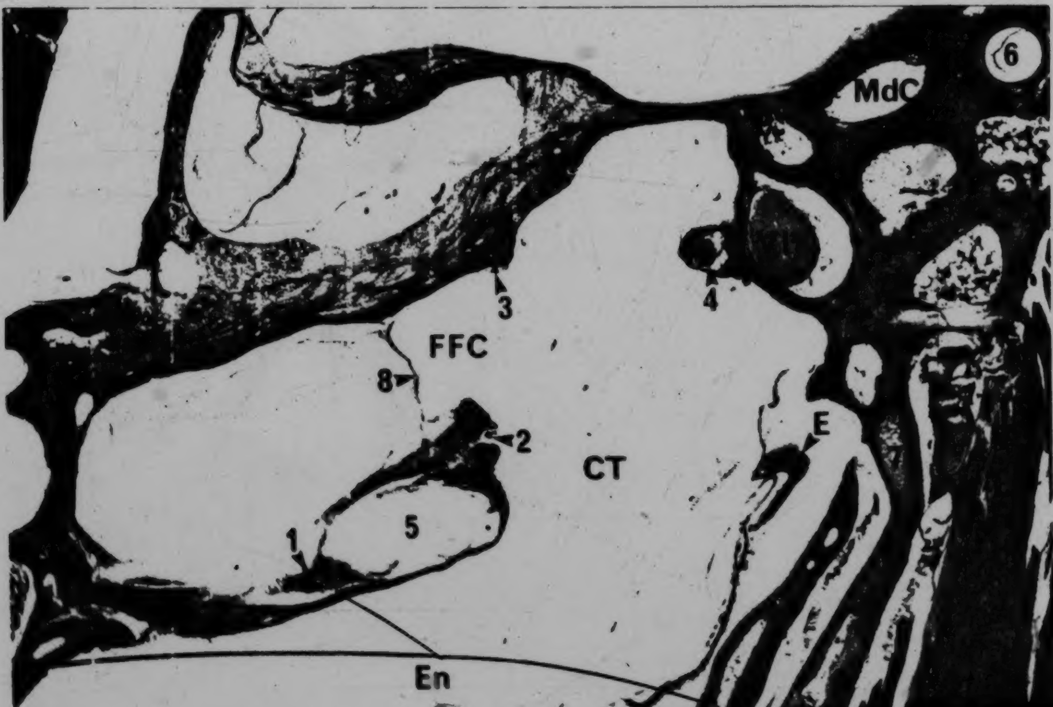

6
MdC
3
4
FFC
8
2
E
CT
5
1
En

FIG. IV-42 *Ptilocercus lowii* USNM 112611 (adult); right auditory region, lateral aspect.

Note the large tympanic process of the alisphenoid, which is not found in Tupaiinae.

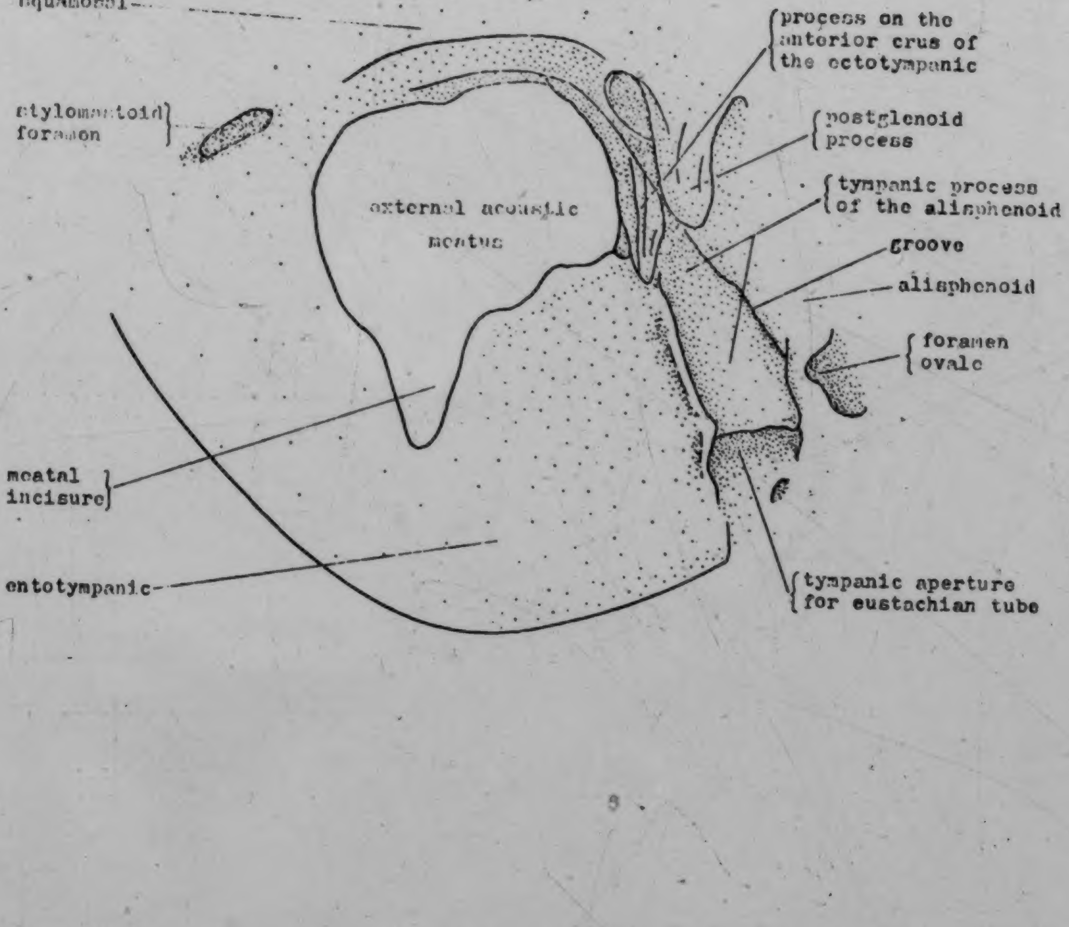

squamosal
stylomastoid foramen
external acoustic meatus
meatal incisure
entotympanic
process on the anterior crus of the ectotympanic
postglenoid process
tympanic process of the alisphenoid
groove
alisphenoid
foramen ovale
tympanic aperture for eustachian tube

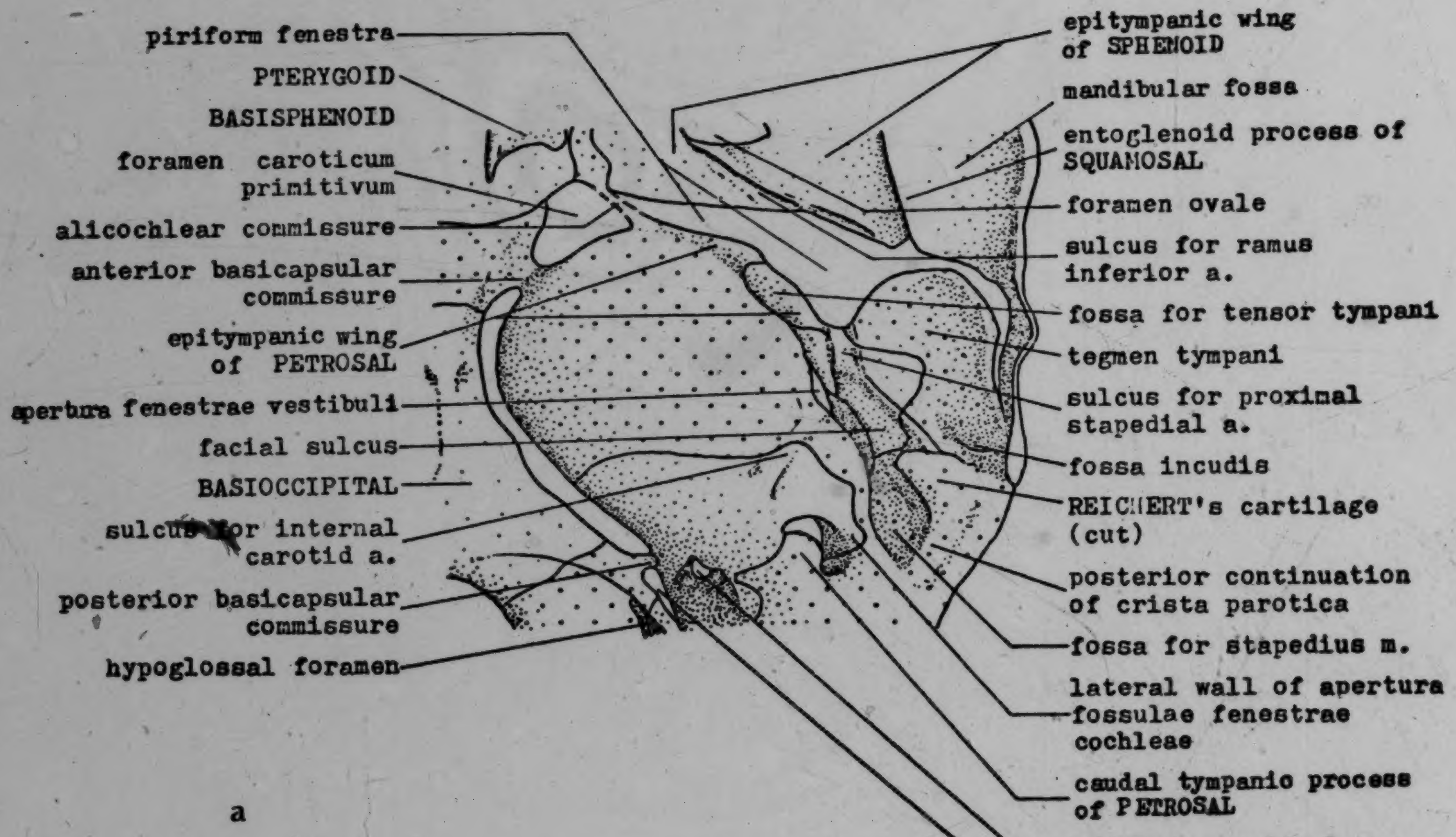
FIG. V-1 *E. fuscipes* MPIH 311/E1 (fetus). Reconstruction of left auditory region and associated structures, ca. x 20. See fig. II-1 for shading conventions.

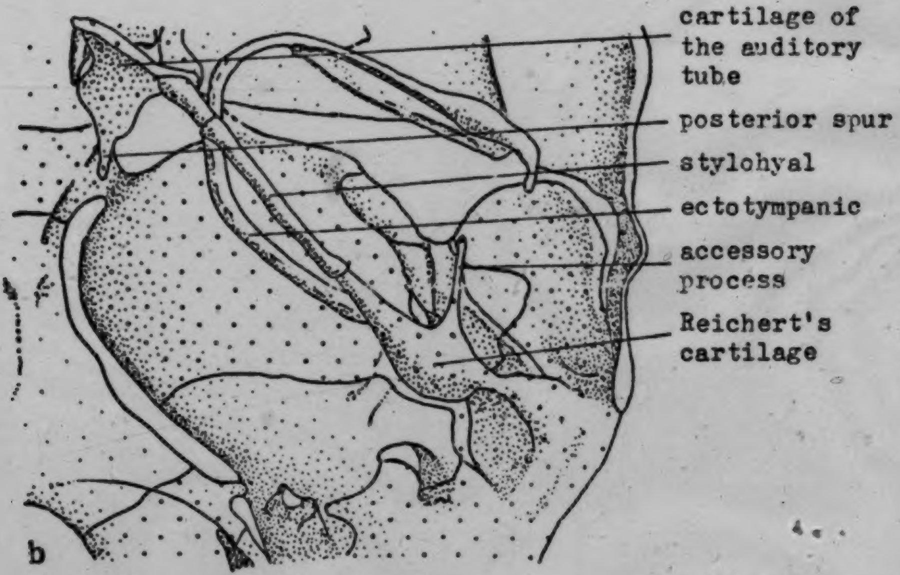
a. General anatomy.

b. Ectotympanic, Reichert's cartilage and cartilage of the auditory tube *in situ*.

c. Routes of arteries and nerves.

The entotympanics and the rostral tympanic process of the petrosal are absent at this stage of development. The caudal tympanic process of the petrosal is represented only by its medial section, and the entoglenoid process of the squamosal is barely indicated. Other bullar components cannot be distinguished.


piriform fenestra
PTERYGOID
BASISPHENOID
foramen caroticum primitivum
alicochlear commissure
anterior basicapsular commissure
epitympanic wing of PETROSAL
apertura fenestrae vestibuli
facial sulcus
BASIOCCIPITAL
sulcus for internal carotid a.
posterior basicapsular commissure
hypoglossal foramen
epitympanic wing of SPHENOID
mandibular fossa
entoglenoid process of SQUAMOSAL
foramen ovale
sulcus for ramus inferior a.
fossa for tensor tympani
tegmen tympani
sulcus for proximal stapedial a.
fossa incudis
REICHERT's cartilage (cut)
posterior continuation of crista parotica
fossa for stapedius m.
lateral wall of apertura fossulae fenestrae cochleae
caudal tympanic process of PETROSAL
cochlear canaliculus
fissura metotica
a


cartilage of the auditory tube
posterior spur
stylohyal
ectotympanic
accessory process
Reichert's cartilage
b

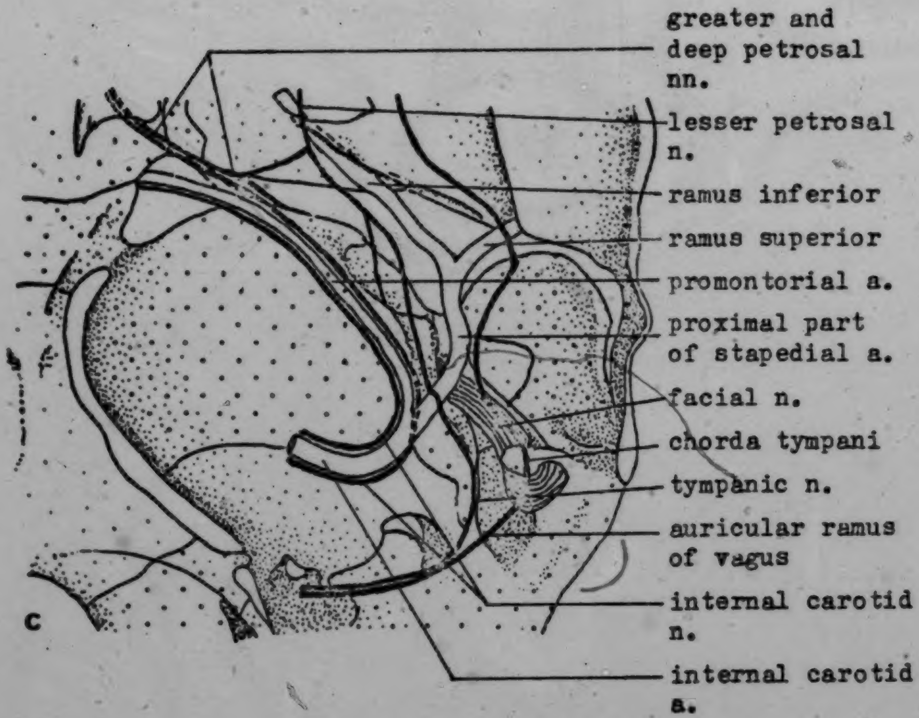

greater and deep petrosal nn.
lesser petrosal n.
ramus inferior
ramus superior
promontorial a.
proximal part of stapedial a.
facial n.
chorda tympani
tympanic n.
auricular ramus of vagus
internal carotid n.
internal carotid a.
c

FIG. V-2 E. rozeti adult. General view of left auditory region; depicted from the posteroventral aspect, in order to expose the position of the tympanic end of the pterygoid canal.

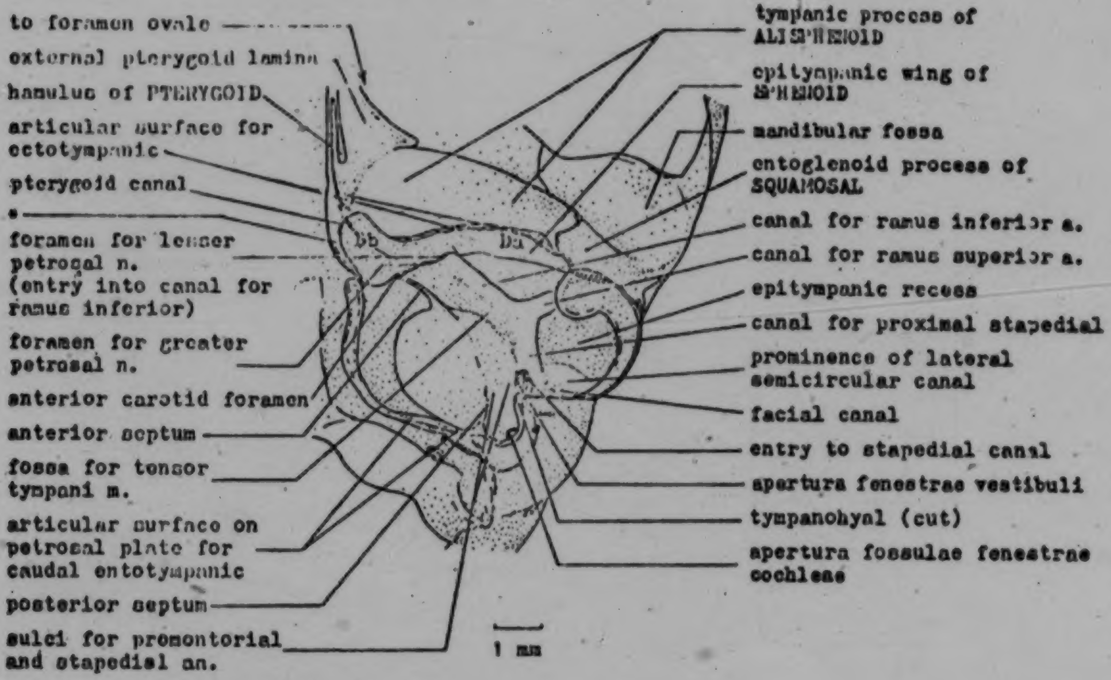
The caudal entotympanic and most of the ectotympanic have been removed (cf. fig. V-3). Designations of diverticula (Da, Db) are those of SABAN (1956-57). Diverticulum D_3 is very small and is covered by the section of the petrosal plate derived from the caudal tympanic process of the petrosal; it is not visible in this illustration. It lies behind the apertura fossulae fenestrae cochleae, as usual.

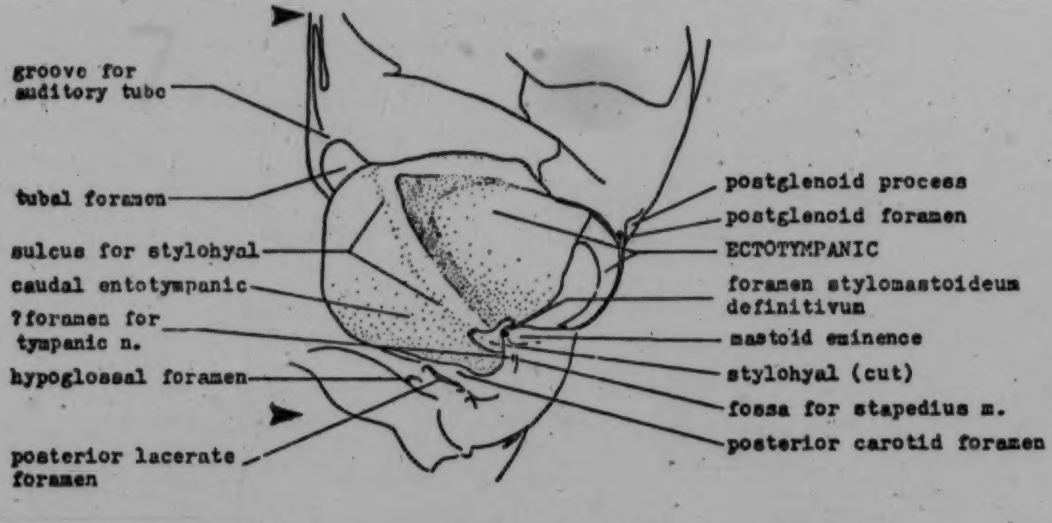
*, tympanic process of the basisphenoid.

FIG. V-3 E. rozeti adult. This illustration is identical to fig. V-2 except that here the fused caudal entotympanic-ectotympanic is shown in situ.

The boundary between the elements originally lay along or near the shallow sulcus for the stylohyal (most of which has been cut away).

FIG. V-4 E. rozeti adult. Medial wall of the bulla as seen from the mid-sagittal plane. The area included in this figure is indicated by the arrows in fig. V-3.


to foramen ovale
external pterygoid lamina
hamulus of PTERYGOID
articular surface for ectotympanic
pterygoid canal
*
foramen for lesser petrosal n. (entry into canal for ramus inferior)
foramen for greater petrosal n.
anterior carotid foramen
anterior septum
fossa for tensor tympani m.
articular surface on petrosal plate for caudal entotympanic
posterior septum
sulci for promontorial and stapedial aa.
1 mm
tympanic process of ALISPHENOID
epitympanic wing of SPHENOID
mandibular fossa
entoglenoid process of SQUAMOSAL
canal for ramus inferior a.
canal for ramus superior a.
epitympanic recess
canal for proximal stapedial
prominence of lateral semicircular canal
facial canal
entry to stapedial canal
apertura fenestrae vestibuli
tympanohyal (cut)
apertura fossulae fenestrae cochleae


groove for auditory tube
tubal foramen
sulcus for stylohyal
caudal entotympanic
?foramen for tympanic n.
hypoglossal foramen
posterior lacerate foramen
postglenoid process
postglenoid foramen
ECTOTYMPANIC
foramen stylomastoideum definitivum
mastoid eminence
stylohyal (cut)
fossa for stapedius m.
posterior carotid foramen

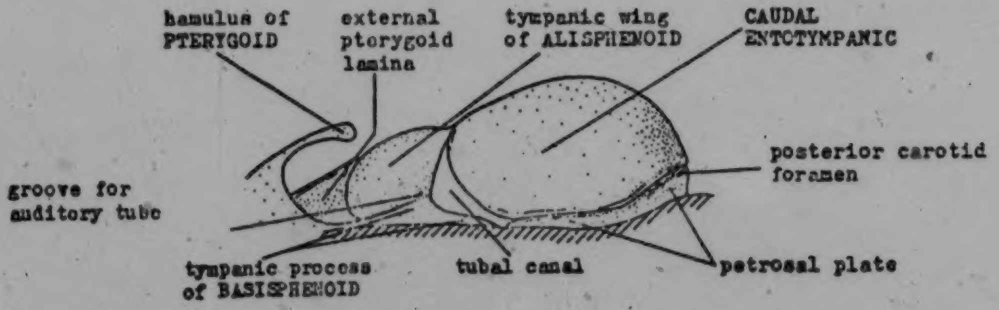

hamulus of PTERYGOID
external pterygoid lamina
tympanic wing of ALISPHENOID
CAUDAL ENTOTYMPANIC
posterior carotid foramen
groove for auditory tube
tympanic process of BASISPHENOID
tubal canal
petrosal plate

FIG. V-5 Development of the bulla in macroscelidean fetuses (adapted from VAN DER KLAAUW 1929). Semidiagrammatic ventral views; only the components of the bulla have been reconstructed.

I - Rhynchocyon sp.; II - Macroscelides ?rozeti; III - Macroscelides sp.; IV - Petrodromus sultani; V - Rhynchocyon sp.; VI - Petrodromus sultani; VII - Macroscelides brachyrynchus.

In the catalogue of the Hubrecht Laboratory (BOTERENBROOD 1977), specimen II is now listed as Elephantulus rozeti and specimen VII as Elephantulus brachyrhynchus. In order to avoid confusion, the taxon names used by VAN DER KLAAUW (1929) are used in the text.

a.c., accessory cartilage; a.m.c.t. anterior margin of cartilage of auditory tube; c.e., caudal entotympanic; c.t., cartilage of auditory tube; e., ectotympanic; e.p.s., entoglenoid process of squamosal; p.t.b., tympanic process of the basisphenoid (may include pterygoidal material as well); p.t.p.c., caudal tympanic process of petrosal; p.t.p.r., rostral tympanic process of petrosal; t.p.a., tympanic process of alisphenoid; r.e., rostral entotympanic.

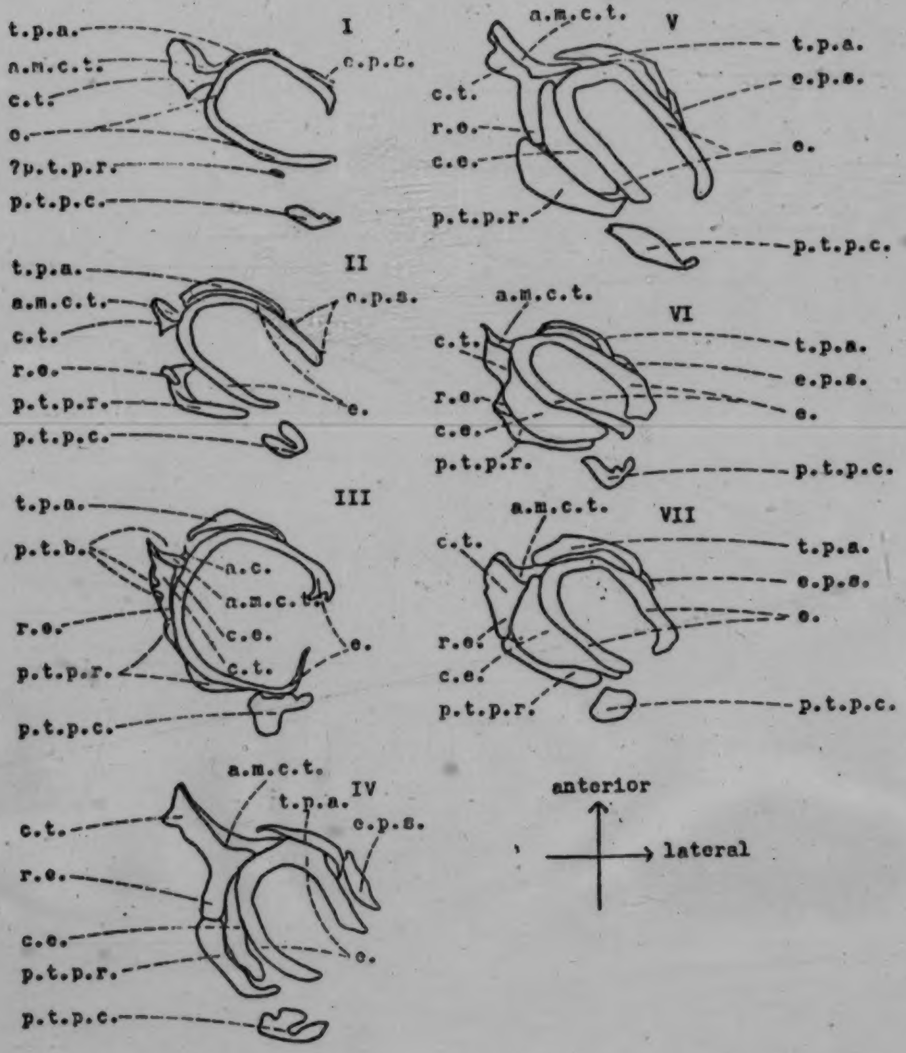

I
t.p.a.
a.m.c.t.
c.t.
e.
?p.t.p.r.
p.t.p.c.
e.p.s.
II
t.p.a.
a.m.c.t.
c.t.
r.e.
p.t.p.r.
p.t.p.c.
e.p.s.
e.
III
t.p.a.
p.t.b.
a.c.
a.m.c.t.
c.e.
c.t.
r.e.
p.t.p.r.
e.
p.t.p.c.
IV
a.m.c.t.
t.p.a.
e.p.s.
c.t.
r.e.
c.e.
p.t.p.r.
e.
p.t.p.c.
V
a.m.c.t.
c.t.
r.e.
c.e.
p.t.p.r.
t.p.a.
e.p.s.
e.
p.t.p.c.
VI
a.m.c.t.
c.t.
r.e.
c.e.
p.t.p.r.
t.p.a.
e.p.s.
e.
p.t.p.c.
VII
a.m.c.t.
c.t.
r.e.
c.e.
p.t.p.r.
t.p.a.
e.p.s.
e.
p.t.p.c.
anterior
lateral

FIG. V-6 *E. fuscipes* MPIH 311/E1 (fetus); s. 1100, cross-section, right side (sides rev.); Azan; x 44.

Anterior (pharyngeal) section of the cartilage of the auditory tube. The nerves of the pterygoid canal pass between the sphenoid and the posterior end of the pterygoid (which is still free at this stage of development). The ramus inferior issues into the temporal fossa adjacent to foramen ovale.

For key to numbered structures, see fig. V-7.

FIG. V-7 *E. fuscipes* MPIH 311/E1 (fetus); s. 1120, cross-section, right side (sides rev.); Azan; x 44.

The tympanic process of the alisphenoid partly arises from the ridge (6) which borders the sulcus for the ramus inferior a., although this is not particularly evident at this stage.

1, ramus inferior of the stapedial a.; 2, lesser petrosal n.; 3, nerves of the pterygoid canal; 4, chorda tympani; 5, gonial; 6, ridge on sulcus for ramus inferior a.; 7, ala temporalis.

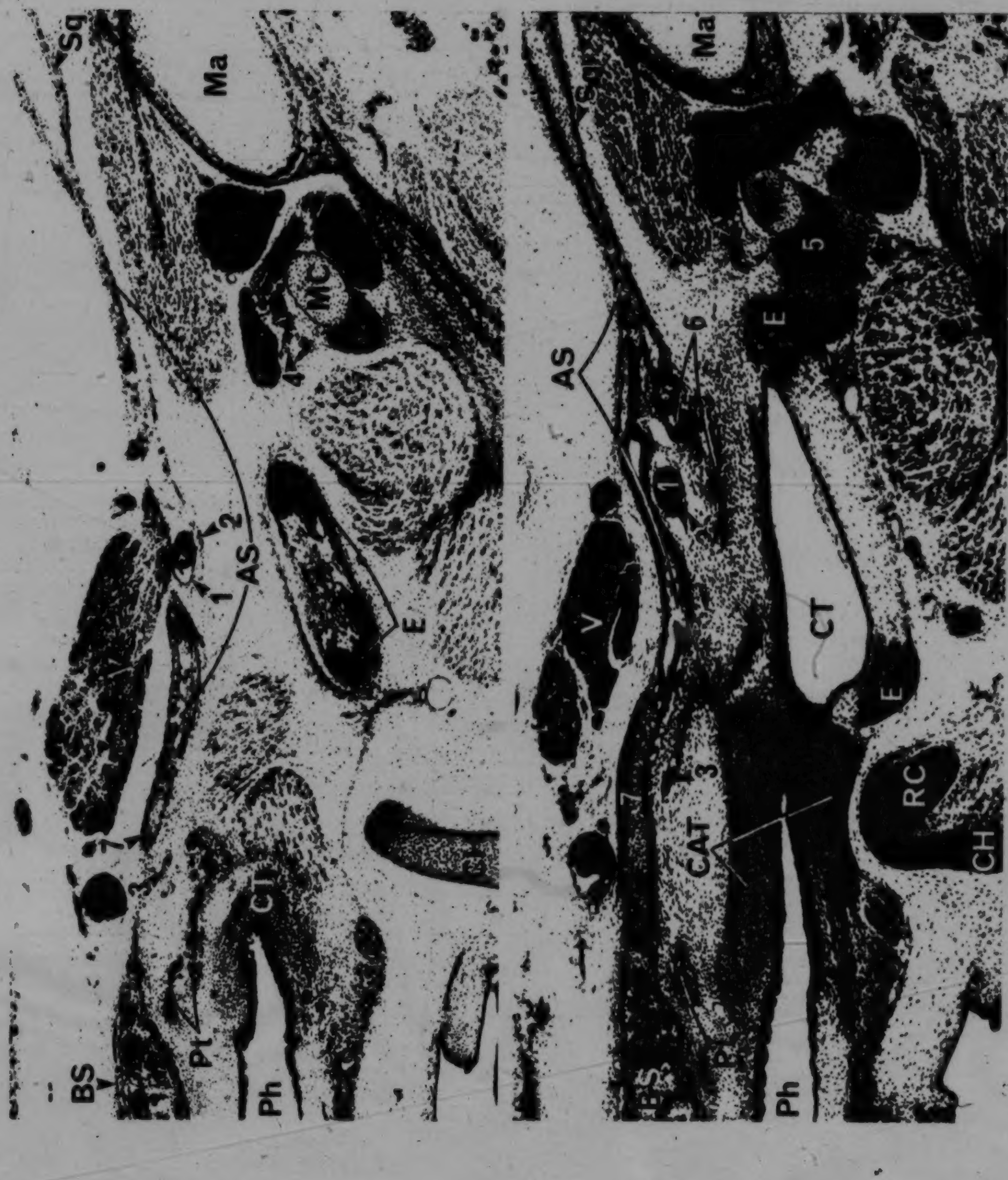

Sq
Ma
MC
4
AS
2
1
E
V
7
3
CT
BS
Pt
Ph
Ma
Sq
AS
6
5
E
1
CT
V
E
RC
3
7
CAT
CH
BS
Pt
Ph

FIG. V-8 E. fuscipes MPIH 311/E1 (fetus); s. 1130, cross-section, right side (sides rev.); Azan; x 44.

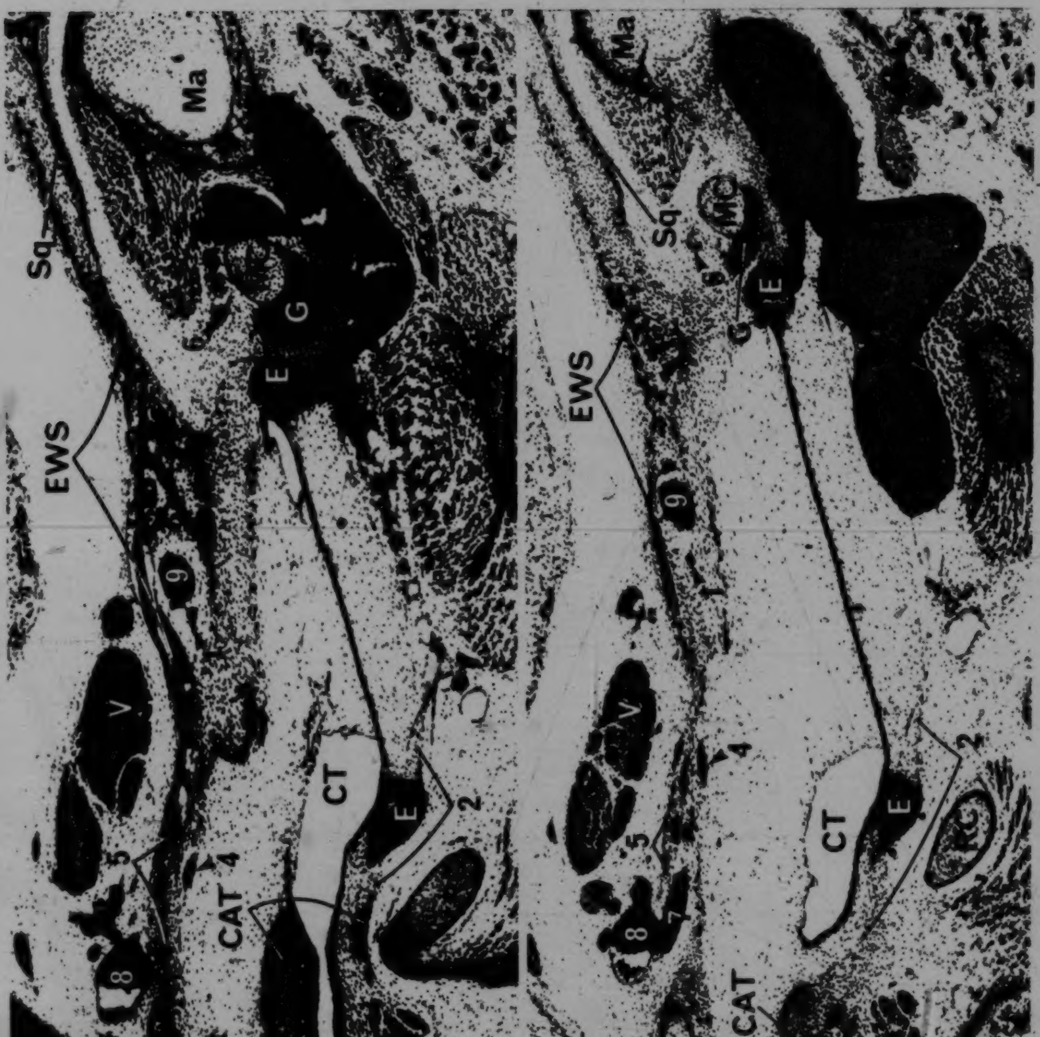
Section through pharyngeal and tympanic apertures of the auditory tube. The reflected anterior margin of the cartilage of the auditory tube ends at this point, but the dorsal part of the cartilage extends further posteriorly.

1, lesser petrosal n.; 2, FMTC; 3, lumen of auditory tube; 4, nerves of pterygoid canal; 5, alicochlear commissure (degenerating); 6, chorda tympani; 7, promontorial a. passing through foramen caroticum primitivum; 8, cavernous sinus; 9, ramus inferior of stapedial a.

FIG. V-9 E. fuscipes MPIH 311/E1 (fetus); s. 1150, cross-section, right side (sides rev.); Azan; x 44.

Section through foramen caroticum primitivum. The alicochlear commissure is degenerating. The fibrous membrane is poorly defined anteriorly.

For key to numbered structures, see fig. V-8.


Sq
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BS
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Sq
MC
E
G
EWS
9
V
5
4
8
7
CT
E
2
RC
CAT
Ph

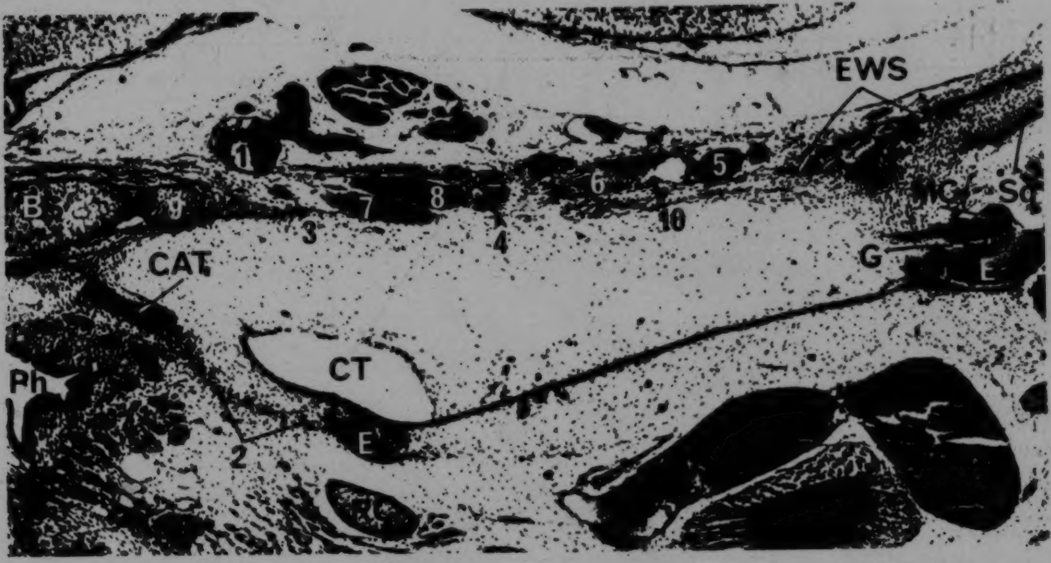
FIG. V-10 _E. fuscipes_ MPIH 311/E1 (fetus); s. 1160, cross-section, right side (sides rev.); Azan; x 44.

Posterior part of the cartilage of the auditory tube, embedded in fibrous membrane of tympanic cavity. Stylohyal center visible in Reichert's cartilage.

1, cavernous sinus; 2, FMTC; 3, part of internal carotid n.; 4, meeting of deep petrosal n. (from internal carotid n.) and greater petrosal n; 5, ramus inferior of stapedial a.; 6, alicochlear commissure; 7, promontorial a.; 8, vein (to cavernous plexus); 9, anterior basicapsular commissure ; 10, lesser petrosal n.

FIG. V-11 _E. fuscipes_ MPIH 311/E1 (fetus); s. 1190, cross-section, right side (sides rev.); Azan; x 117.

Section through posterior spur of the cartilage of the auditory tube. Anlage of caudal entotympanic not evident within fibrous membrane of the tympanic cavity at this stage of development.


EWS
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B
9
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3
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10
MC
Sc
CAT
G
E
CT
Ph
2
E

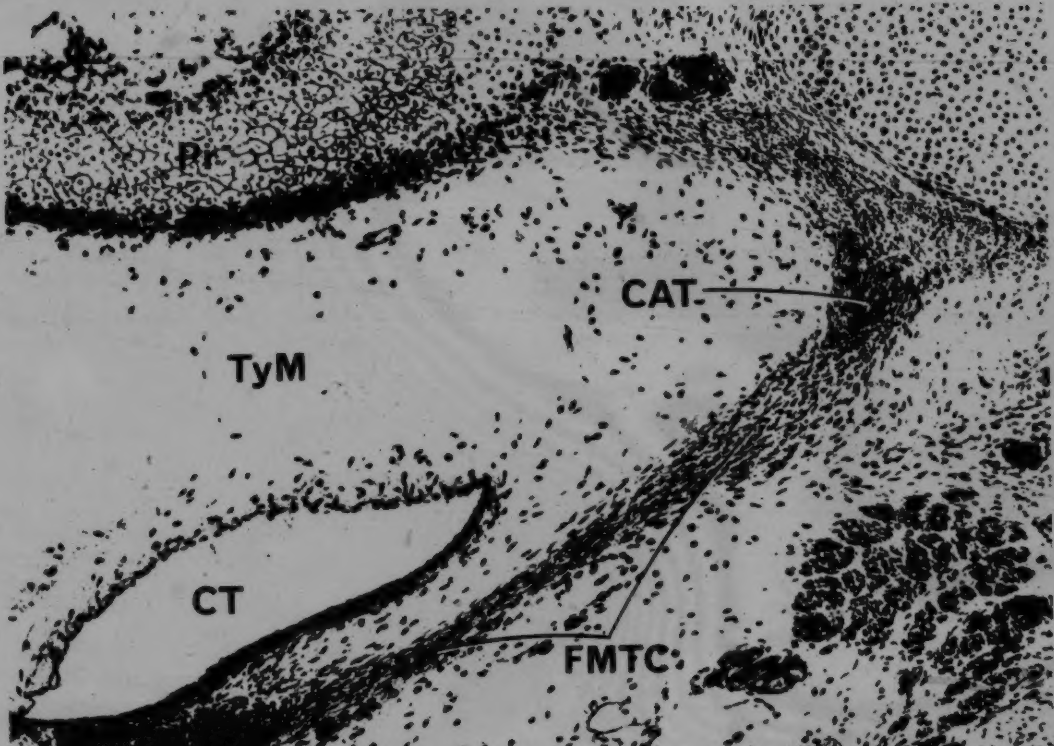

Pr
CAT
TyM
CT
FMTC
E

FIG. V-12 *E. fuscipes* MPIH 311/E1 (fetus); s. 1290, cross-section right side (sides rev.); Azan; x 86.

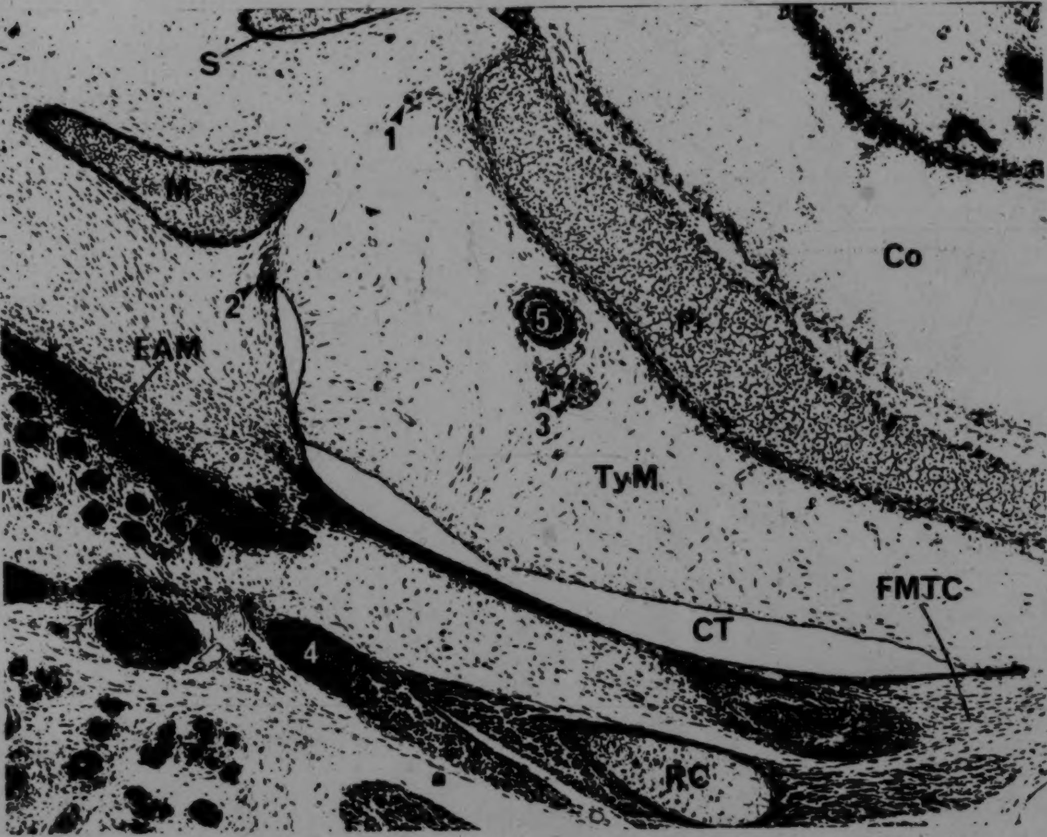
Accessory process of Reichert's cartilage. This process is not closely associated with the chorda tympani and is therefore unlikely to be an element of Spence.

1, tympanic n.; 2, chorda tympani; 3, divisions of internal carotid n.; 4, accessory process of Reichert's cartilage; 5, promontorial a.

FIG. V-13 *E. fuscipes* MPIH 311/E1 (fetus); s. 1370, cross-section, left side; Azan; x 44.

Section through (membranous) posterior carotid foramen.

1, internal carotid a.; 2, internal carotid n.; 3, local thickening of fibrous membrane of tympanic cavity; 4, tympanic n.


S
1
M
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EAM
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Pr
3
Co
TyM
FMTC
CT
4
RC

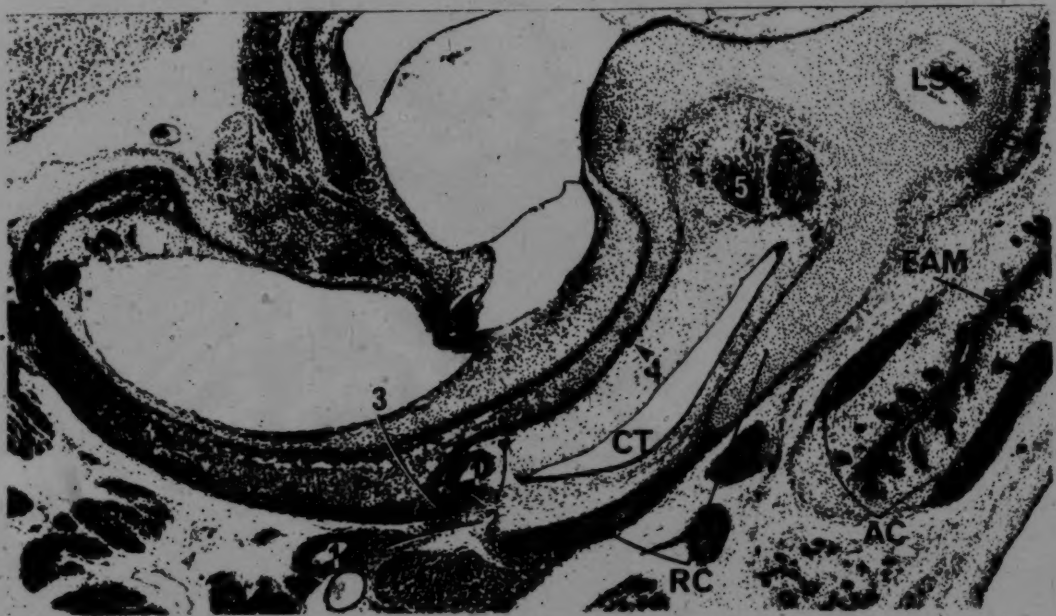

LSC
5
EAM
3
CT
AC
RC

FIG. V-14 *E. fuscipes* MPIH 311/E1 (fetus).

a. s. 1411, cross-section, right side (sides rev.); Cresyl Violet; x 44.

b. s. 1430, cross-section, left side; Azan; x 44.

c. s. 1431, cross-section, right side (sides rev.); Cresyl Violet; x 44.

Series of cross-sections through the posterior part of the tympanic cavity. The medial section of the caudal tympanic process of the petrosal is a lateral prolongation of the processus recessus beneath the apertura fossulae fenestrae cochleae and diverticulum D_3. The massive lateral wall of the apertura forms the medial wall of the fossa for the stapedius muscle. Adult conditions (fig. V-2) indicate that the lateral wall of the apertura eventually forms the rest of the caudal tympanic process of the petrosal, thus enclosing a diverticulum D_3 of very small dimensions. Note that the fibrous membrane of the tympanic cavity attaches to the lateral wall of the apertura, not to the posterior continuation of the crista parotica. As a result, the origin of the stapedius muscle is excluded from the presumptive tympanic cavity.

1, perilymphatic duct; 2, lateral wall of fossula fenestrae cochleae; 3, posterior continuation of crista parotica; 4, caudal tympanic process of petrosal (medial section); 5, FMTC; 6, auricular ramus of vagus; 7, tympanic n. (travelling with ramus auricularis); 8, stapedius m.; 9, internal jugular v.

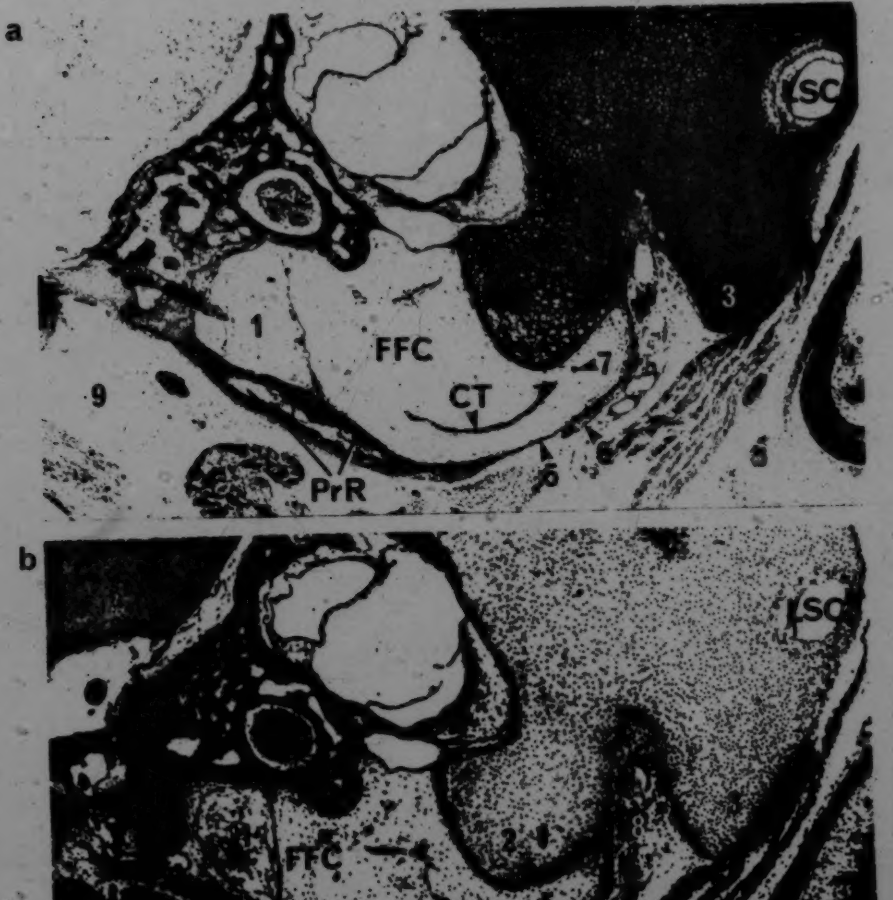

a
LSC
1
FFC
7
CT
9
PrR
6
6
5
3
b
LSC
2
FFC
CT
5
9
PrR
4
6,7
EAM
c
LSC
3
EO
1
IX,X
D_3
2
4
6,7

FIG. V-15 E. fuscipes MPIH 305/E (fetus); s. 1421, cross-section, left side; Azan; x 44.

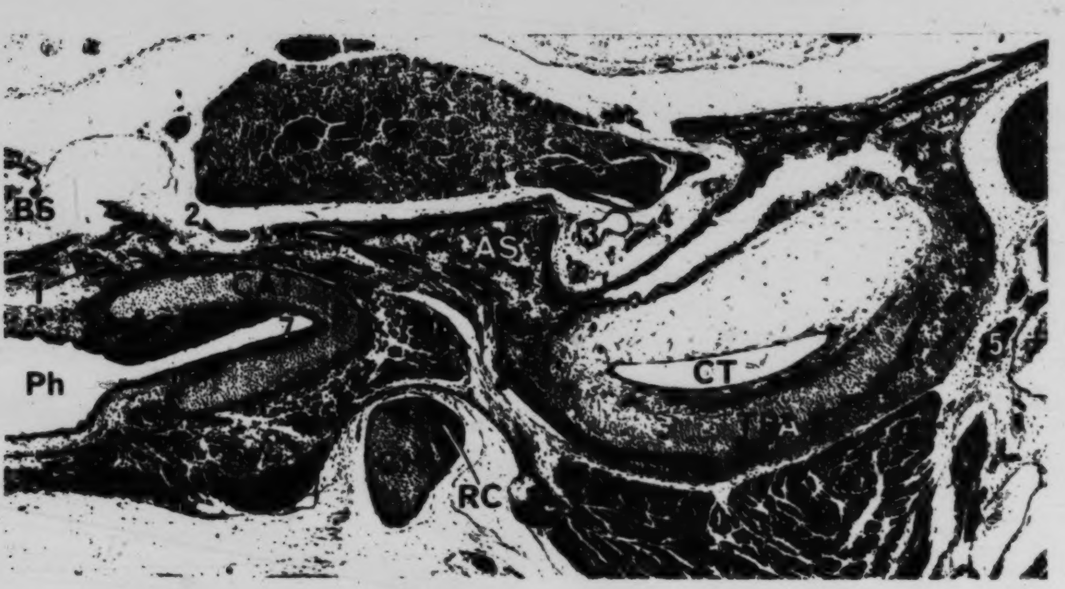
Anterior (pharyngeal) part of the cartilage of the tube and the tympanic process of the alisphenoid. The bone lying beneath the nerves of the pterygoid canal is probably derived from the posterior part of the pterygoid (which is now fused to the sphenoid). Note the small ridge (1) above the pharyngeal aperture of the auditory tube.

1, ridge (rudiment of tympanic process of basisphenoid); 2, nerves of pterygoid canal; 3, ramus inferior of stapedial a.; 4, lesser petrosal n.; 5, chorda tympani; 6, Meckel's cartilage (degenerating); 7, lumen of auditory tube.

FIG. V-16 E. fuscipes MPIH 305/E (fetus); s. 1431, cross-section, left side; Azan; x 44.

Anterior (pharyngeal) part of the cartilage of the tube and the entoglenoid process of the squamosal. The entoglenoid is small at this stage and does not overlap the tympanic process of the alisphenoid.

For key to numbered structures, see fig. V-15.


BS
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AS
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7
Ph
CT
TPA
5
RC

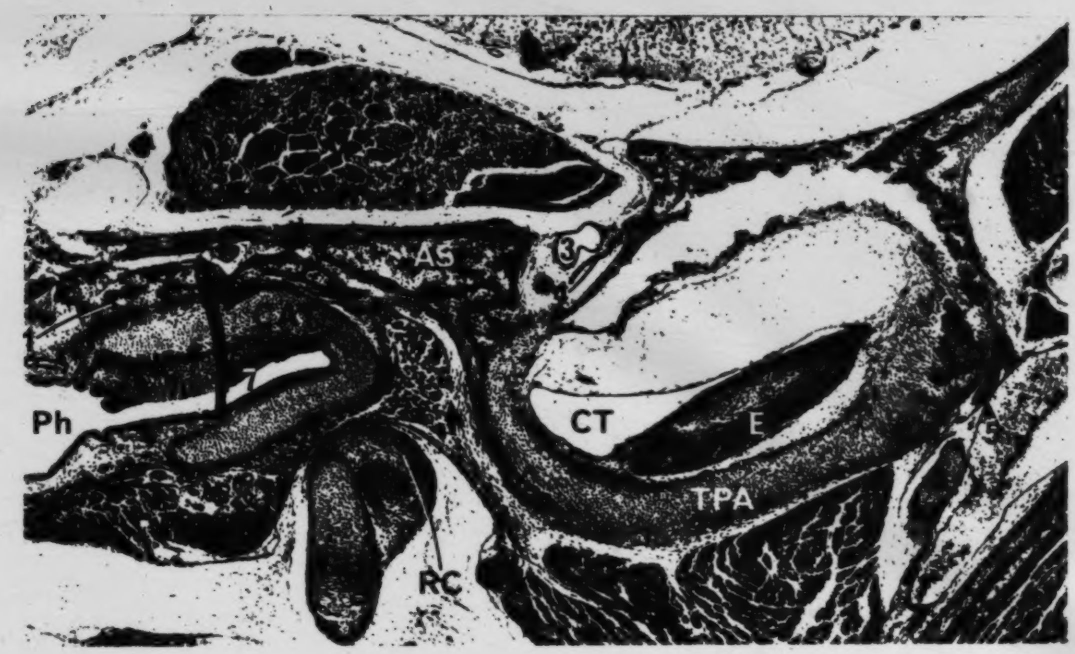

AS
3
1
7
Ph
CT
E
TPA
RC

FIG. V-17 *E. fuscipes* MPIH 305/E (fetus); s. 1481, cross-section, left side; Azan; x 44.

Relationship of the anterior end of the caudal entotympanic and the tubal cartilage.

1, promontorial a. (cerebral carotid a.); 2, nerves of pterygoid canal; 3, chorda tympani; 4, FMTC; 5, lesser petrosal n.; 6, ramus inferior of stapedial a.; 7, lumen of auditory tube; 8, cavernous sinus; 9, ridge (rudiment of tympanic process of basisphenoid).

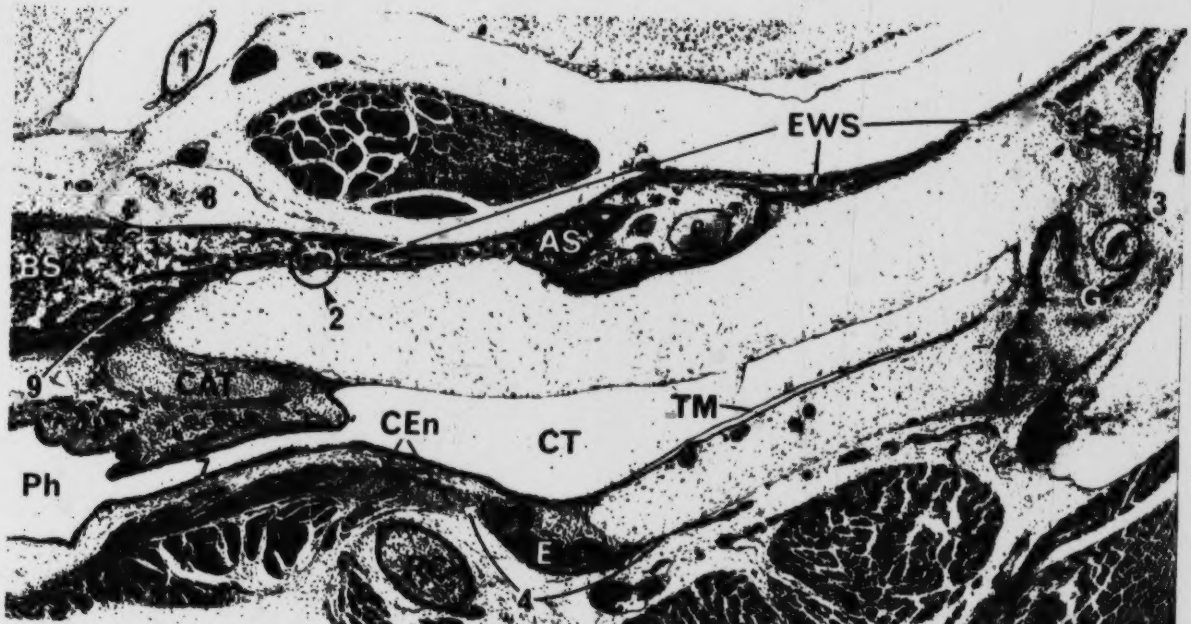

1
EWS
8
BS
AS
3
2
C
9
CAT
TM
CEn
CT
Ph
E
4

FIG. V-18 *E. fuscipes* MPIH 305/E (fetus); s. 1531, cross-section, left side; Azan; x 44.

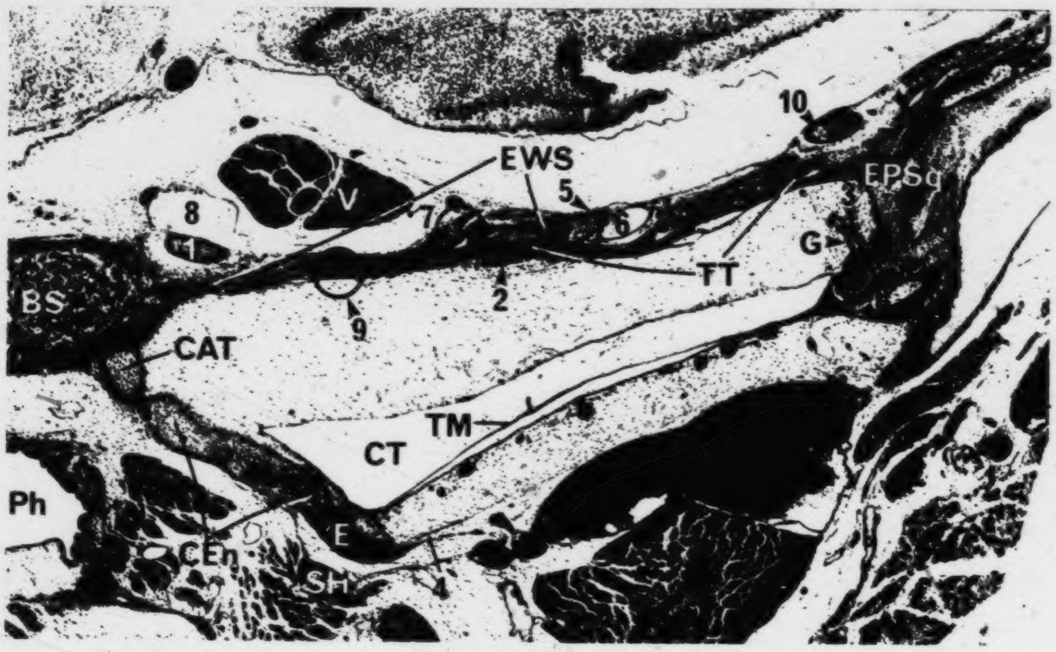
Relationship of the posterior spur of the tubal cartilage and the dorsal margin of the caudal entotympanic. As may be seen in fig. V-17 as well, the two elements are not fused.

1, promontorial a. (cerebral carotid a.); 2, tensor tympani m.; 3, chorda tympani; 4, FMTC; 5, lesser petrosal n.; 6, ramus inferior of stapedial a.; 7, greater petrosal n.; 8, cavernous sinus; 9, deep petrosal n. (from internal carotid n.); 10, ramus superior of stapedial a.; 12, vein (to cavernous sinus).

FIG. V-19 *E. fuscipes* MPIH 305/E (fetus); s. 1558, cross-section; left side; Azan; x 31.

Anterior end of rostral entotympanic.

For key to numbered structures, see fig. V-18.


10
EWS
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EPSq
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V
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1
G
TT
BS
2
9
CAT
TM
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Ph
E
CEn
SH
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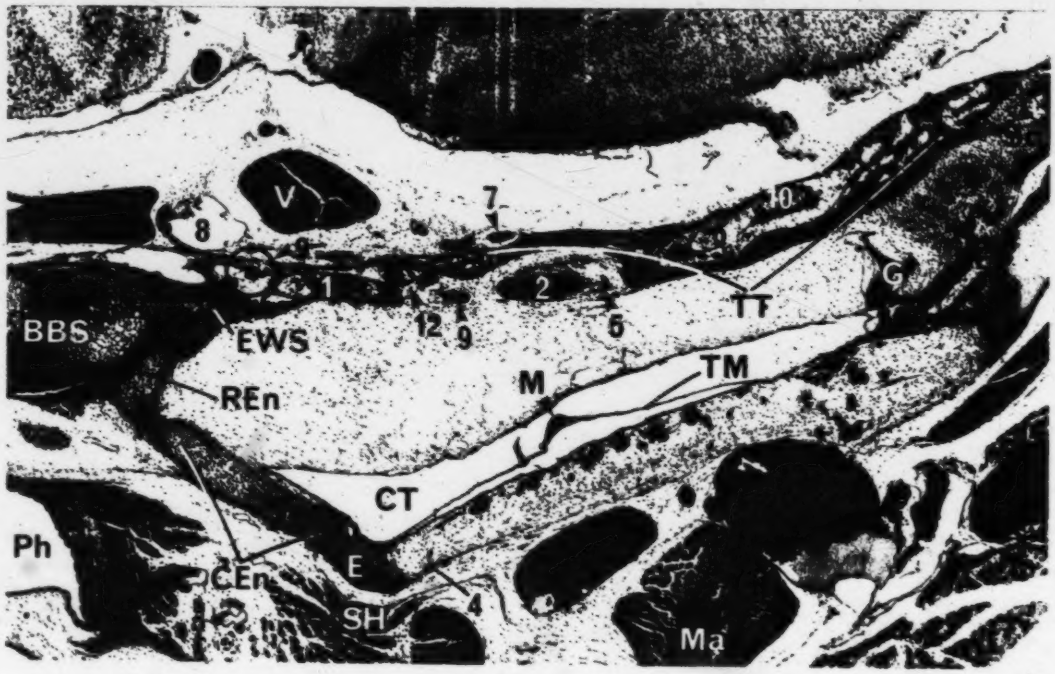
V
7
10
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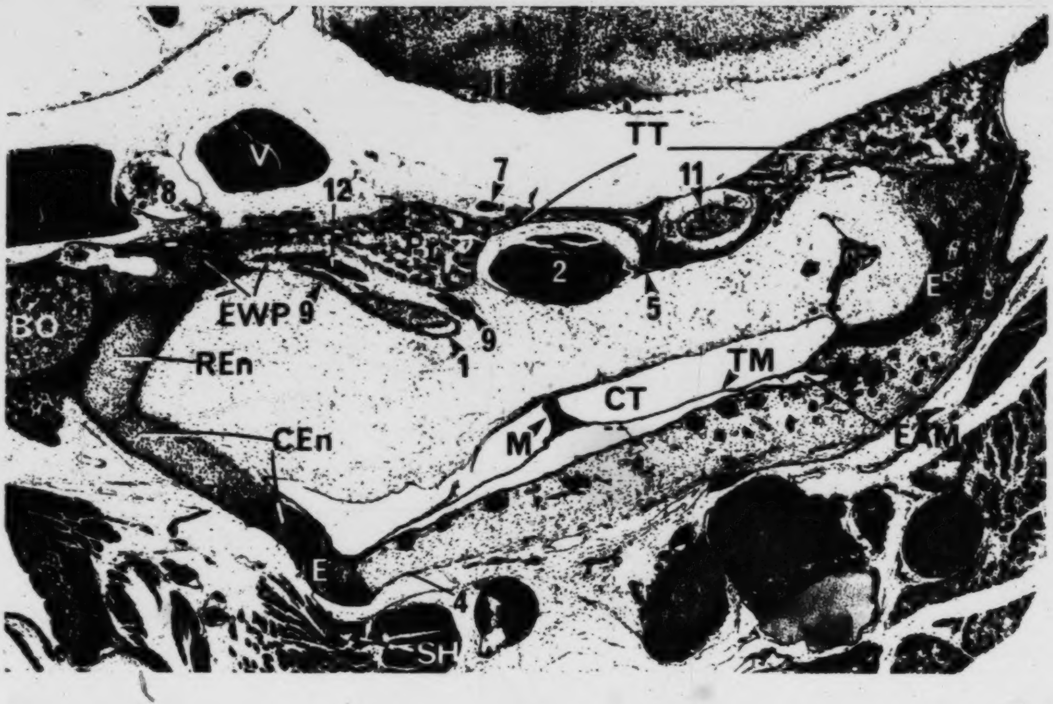
9
1
2
TT
G
BBS
EWS
12
9
5
REn
M
TM
CT
Ph
E
CEn
SH
4
Ma

FIG. V-20 *E. fuscipes* MPIH 305/E (fetus); x. 1581, cross-section, left side; Azan; x 31.

Section through anterior pole of promontory.

For key to numbered structures, see fig. V-18.


V
8
12
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TT
11
2
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E
BO
EWP
9
9
1
REn
TM
CT
M
CEn
EAM
E
4
SH

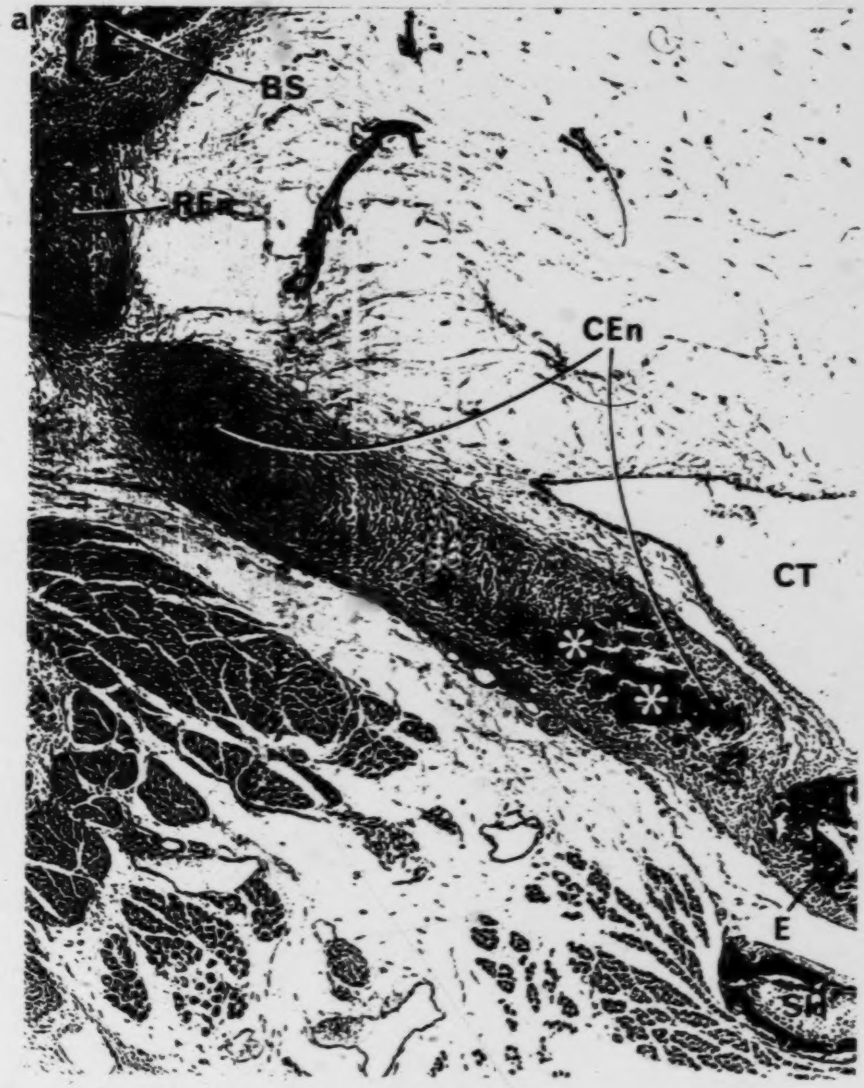
FIG. V-21 *E. fuscipes* MPIH 305/E (fetus).

Visualization of the caudal entotympanic using different histological methods. Black asterisks indicate secondary cartilage and white asterisks indicate bone tissue.

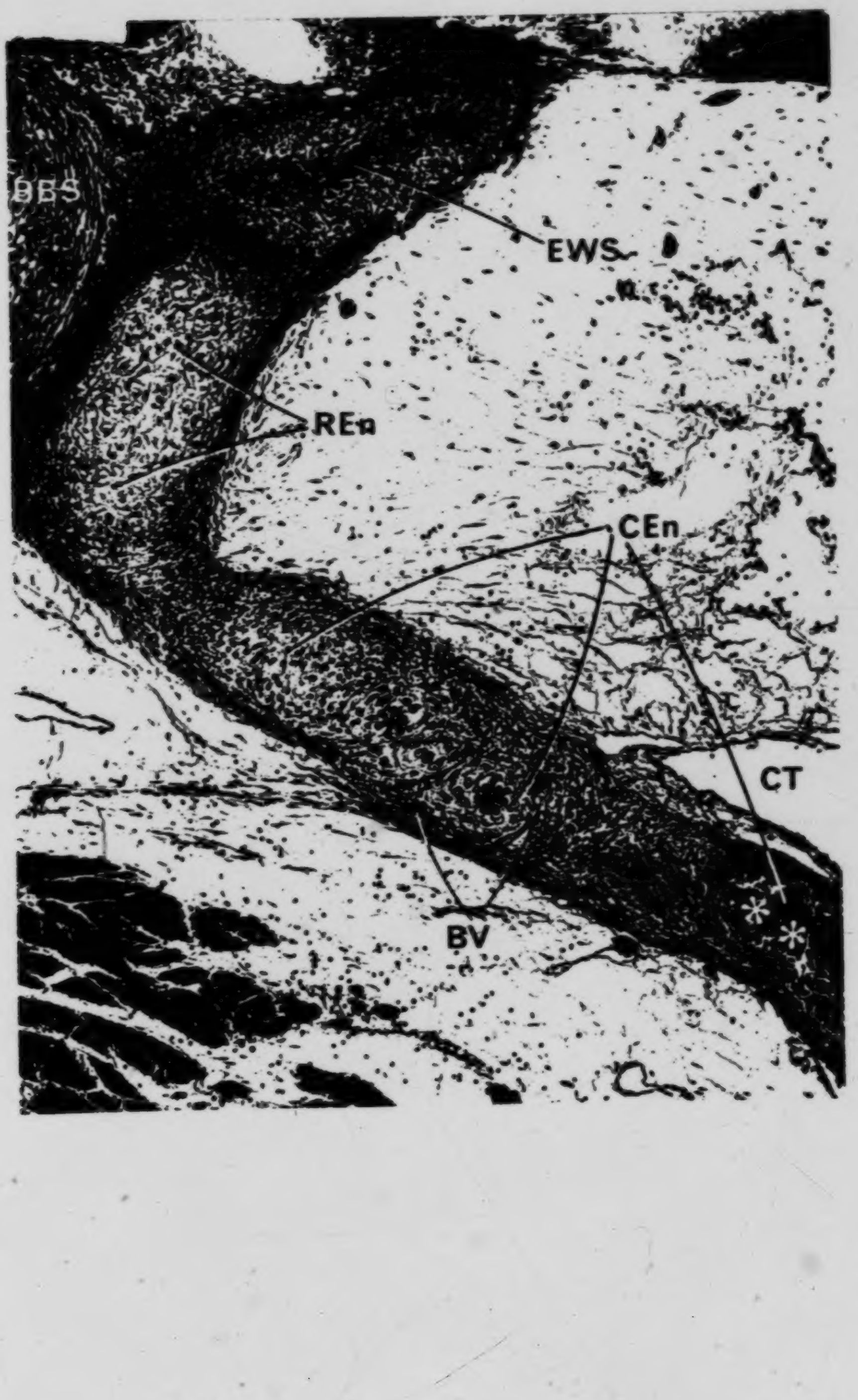
a. s. 1536, cross-section, left side; Periodic Acid-Schiff with Alcian Blue; x 117.

b. s. 1569, cross-section, left side; Azan; x 117.

c. s. 1570, cross-section, left side; Cresyl Violet; x 117.


a
BS
RFn
CEn
CT
*
*
E
SH

b


BBS
EWS
REn
CEn
CT
BV
*
*

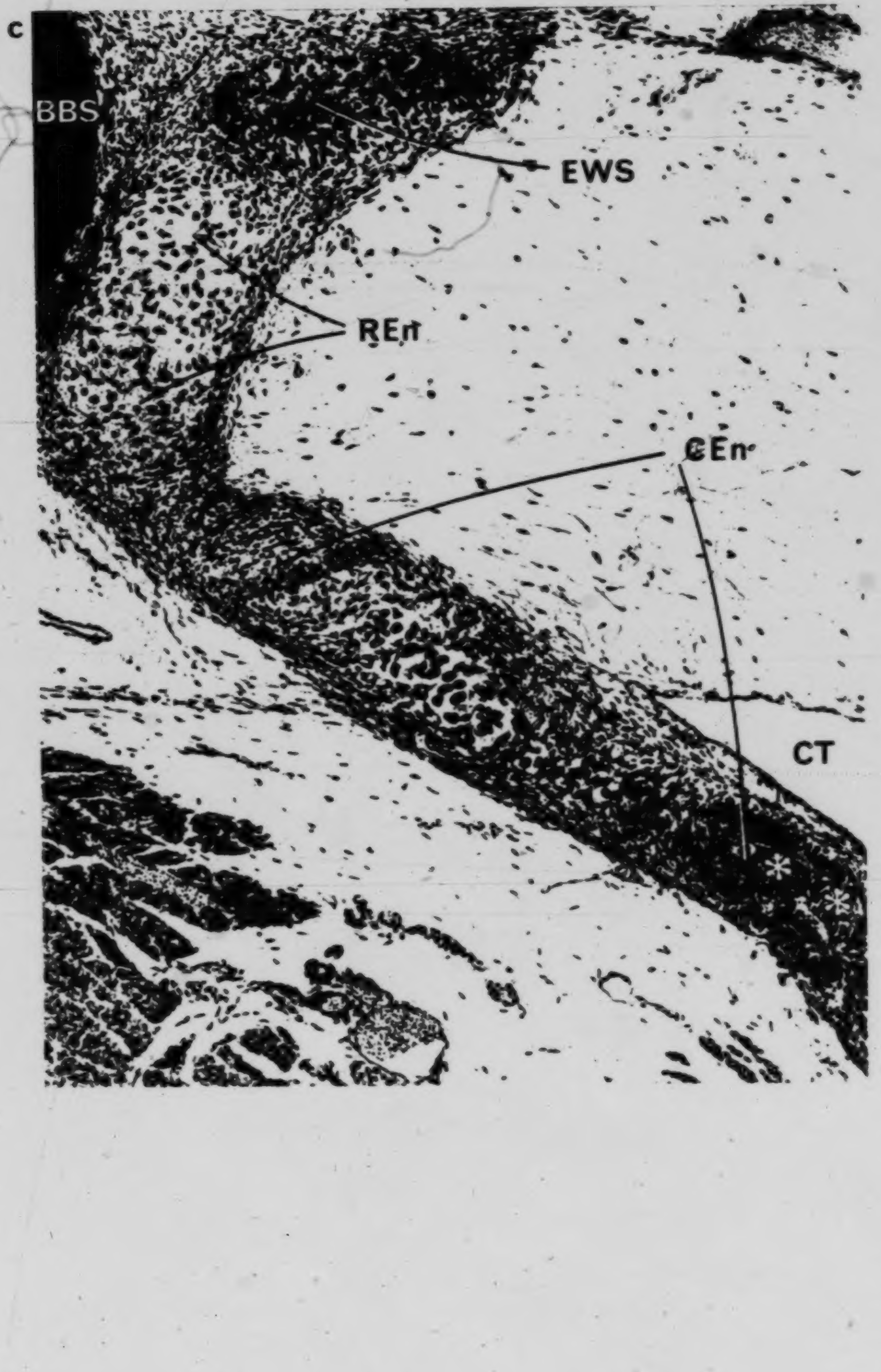

C
BBS
EWS
REn
CEn
CT
*
*

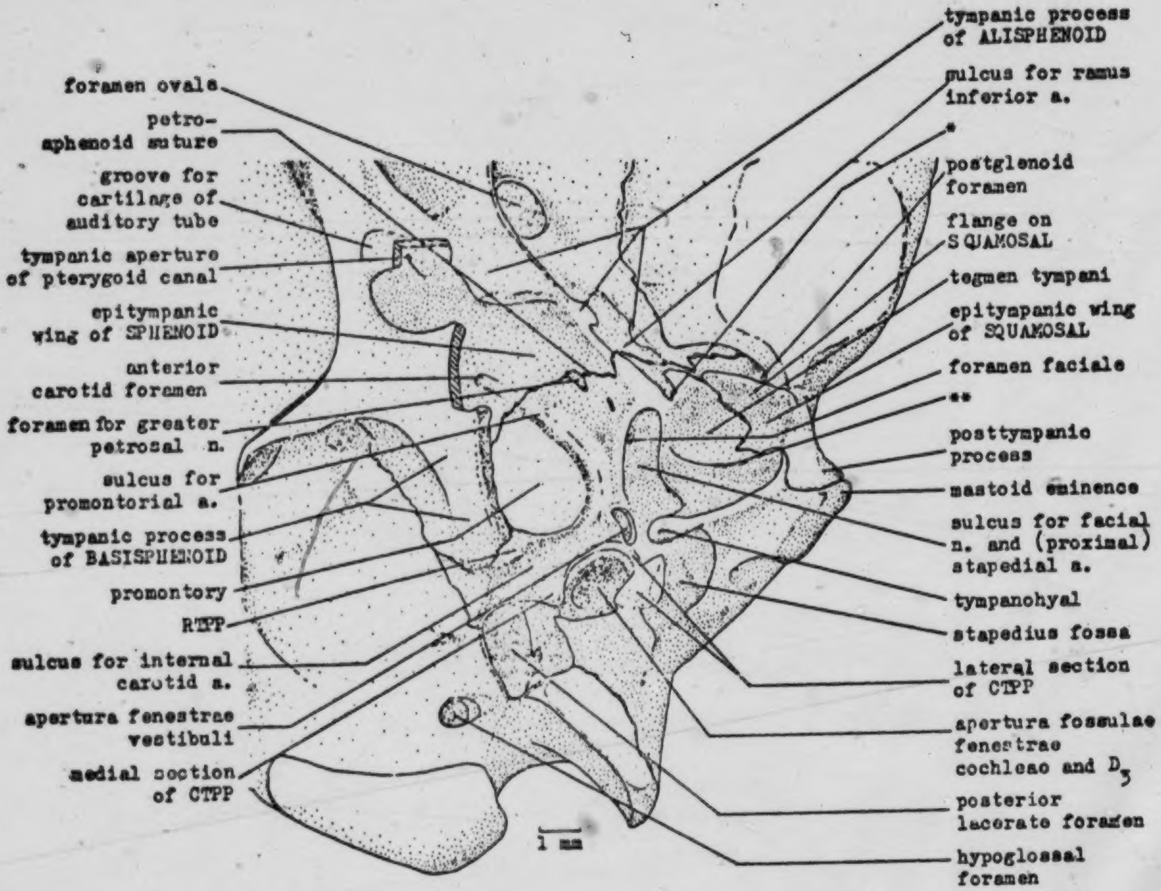
FIG. VI-1 E. europaeus adult. General view of left auditory region, ventral aspect.

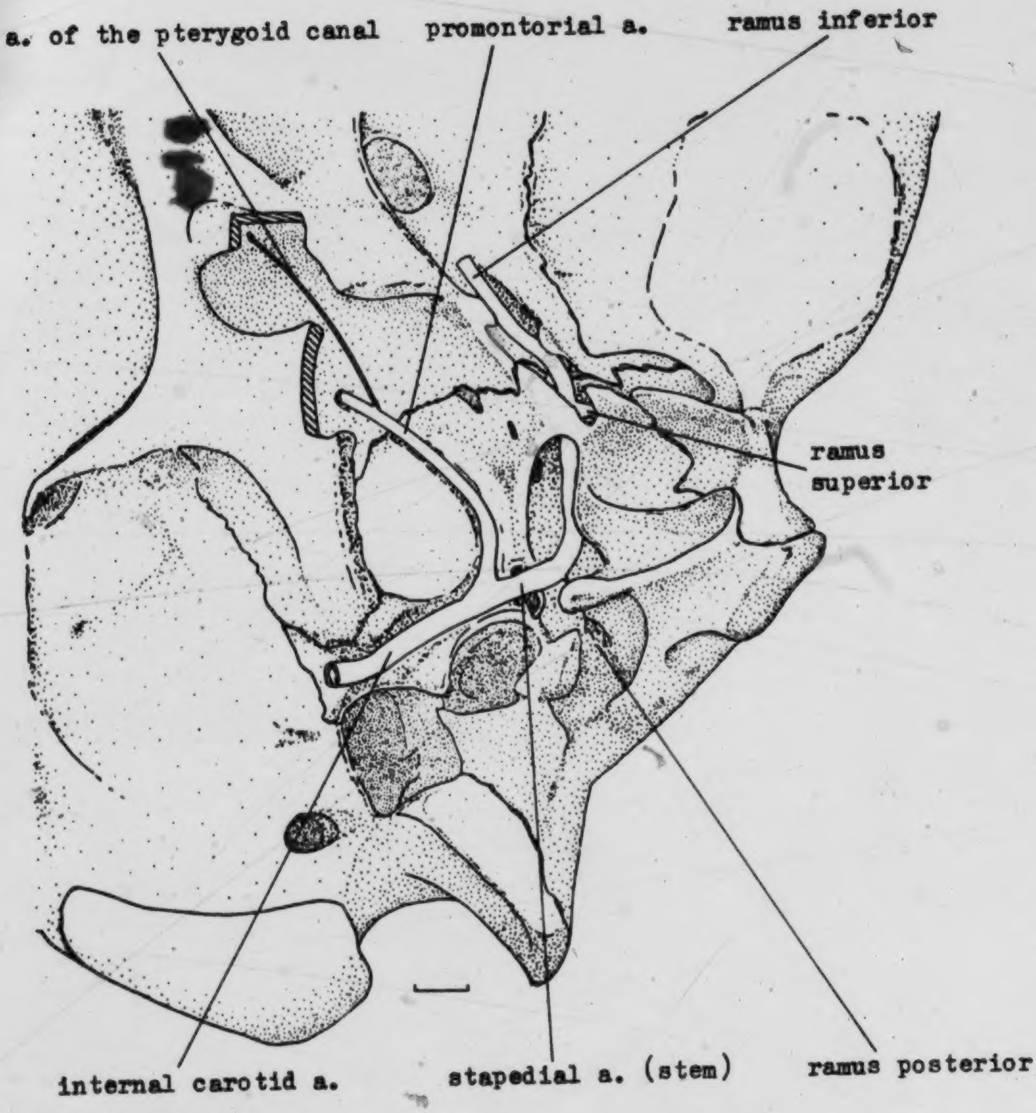
a. General anatomy.

b. Routes of arteries.

The ectotympanic and parts of the tympanic processes of the basisphenoid and alisphenoid have been removed (cf. fig. VI-2). The flange of the squamosal may represent part of the entoglenoid. All that remains of the piriform fenestra is the very large foramen for the greater petrosal n.

*, foramen for ramus superior a. (partly occluded by projecting ridge on tegmen tympani; **, so-called Chordafortsatz; separates epitympanic recess from the accessory cavity excavating a small part of the mastoid eminence.


foramen ovale
petro-sphenoid suture
groove for cartilage of auditory tube
tympanic aperture of pterygoid canal
epitympanic wing of SPHENOID
anterior carotid foramen
foramen for greater petrosal n.
sulcus for promontorial a.
tympanic process of BASISPHENOID
promontory
RTPP
sulcus for internal carotid a.
apertura fenestrae vestibuli
medial section of CTPP
1 mm
tympanic process of ALISPHENOID
sulcus for ramus inferior a.
*
postglenoid foramen
flange on SQUAMOSAL
tegmen tympani
epitympanic wing of SQUAMOSAL
foramen faciale
**
posttympanic process
mastoid eminence
sulcus for facial n. and (proximal) stapedial a.
tympanohyal
stapedius fossa
lateral section of CTPP
apertura fossulae fenestrae cochleae and D_3
posterior lacerate foramen
hypoglossal foramen


a. of the pterygoid canal
promontorial a.
ramus inferior
ramus superior
internal carotid a.
stapedial a. (stem)
ramus posterior

b

2

FIG. VI-2 *E. europaeus* adult. This illustration is identical to fig. VI-1, except that here all structures are complete and the ectotympanic is *in situ*. The ectotympanic is semiphaneric; part of its medial portion is covered by the tympanic process of the basisphenoid.

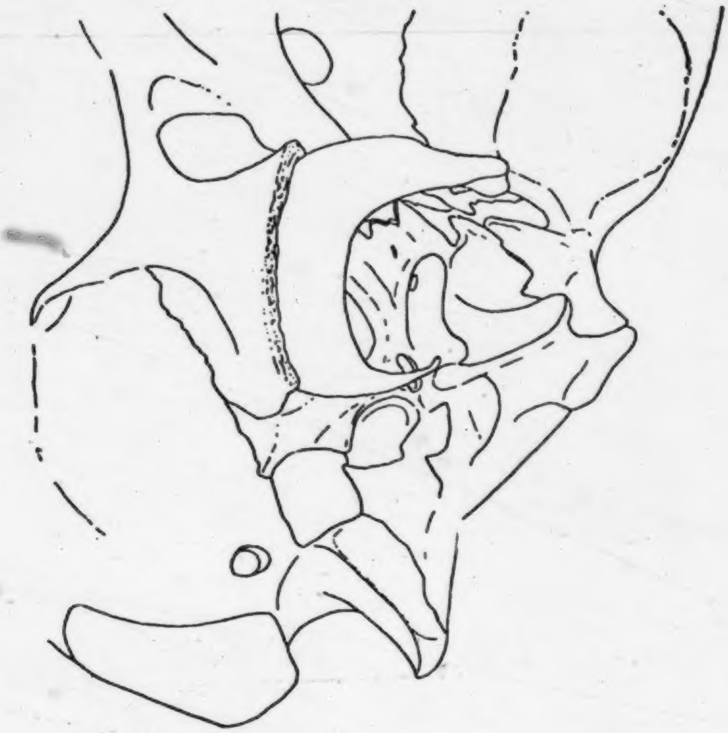
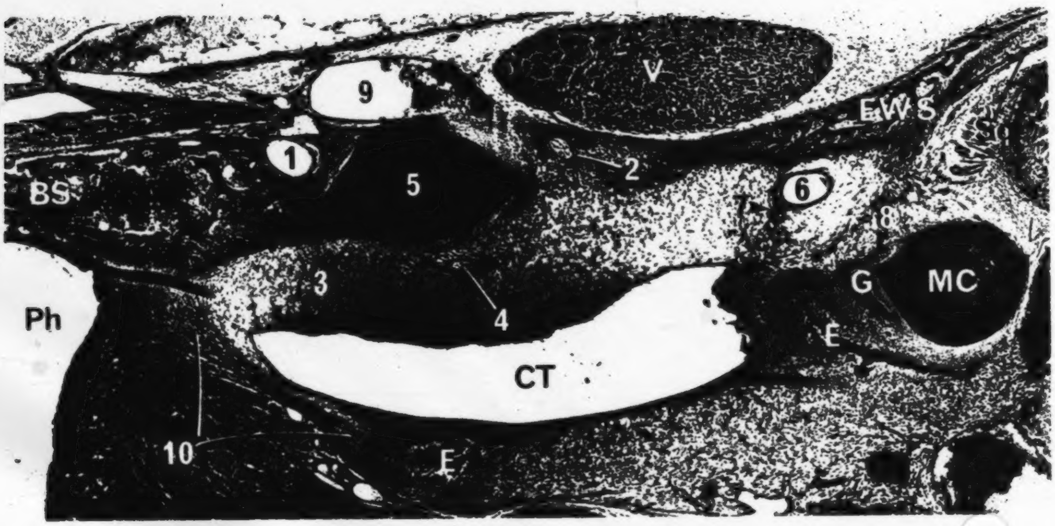


FIG. VI-3 *E. europaeus* MPIH 1964/52b (newborn); s. 1000, cross-section, left side; Klüver-Barrera; x 32.

Anterior end of presumptive tympanic cavity. The pterygoid is fused to the basisphenoid by this stage, but it is still free in the near-term fetus (MPIH 1964/58a; not illustrated).

1, promontorial a. (cerebral carotid a.); 2, lumen of auditory tube; 3, a. of pterygoid canal; 4, nerves of pterygoid canal; 5, ala temporalis and processus alaris; 6, ramus inferior of the stapedial a; 7, lesser petrosal n.; 8, chorda tympani; 9, cavernous sinus; 10, FMTC.


9
V
EWS
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BS
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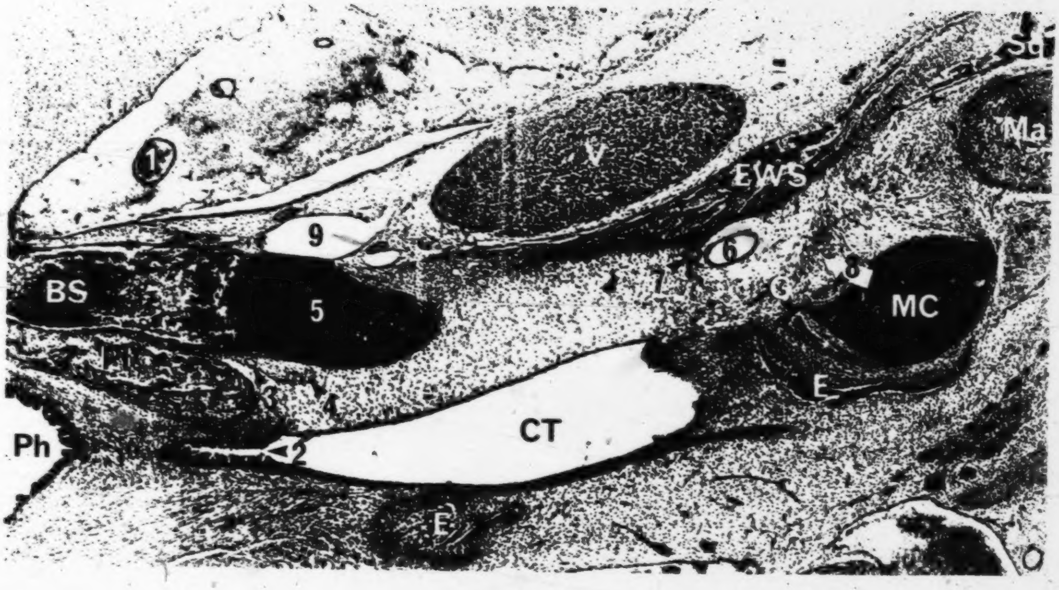
2
6
8
MC
G
Ph
3
4
E
CT
10
E

FIG. VI-4 E. europaeus MPIH 1964/52b (newborn); s. 1040, cross-section, right side (sides rev.); Klüver-Barrera; x 32.

Promontorial a. within foramen caroticum primitivum. Note small a. of the pterygoid canal.

For key to numbered structures, see fig. VI-3.


1
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EWS
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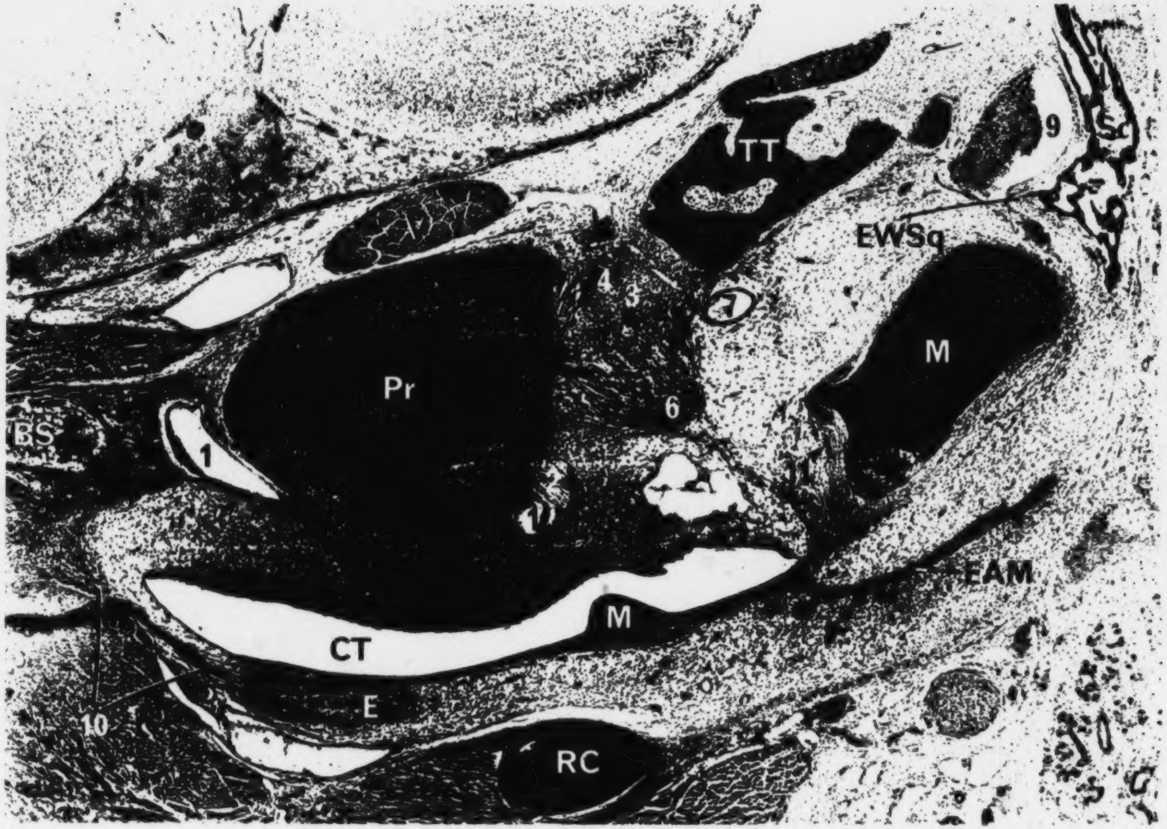
9
6
BS
5
7
G
8
MC
3
4
CT
E
Ph
2
E

FIG. VI-5 E. europaeus MPIH 1964/52b (newborn); s. 1040, cross-section, left side; Klüver-Barrera; x 32.

Anterior pole of promontory. Note peculiar, labyrinthine appearance of tegmen tympani.

1, promontorial a.; 2, internal carotid n.; 3, lesser petrosal n.; 4, greater petrosal n.; 5, geniculate ganglion; 6, tensor tympani m.; 7, ramus inferior of the stapedial a.; 8, ramus superior of the stapedial a.; 9, petrosquamous sinus; 10, fibrous membrane of tympanic cavity; 11, chorda tympani.


TT
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EWSq
4
3
7
M
Pr
6
BS
1
EAM
M
CT
E
10
RC

FIG. VI-6 *E. europaeus* MPIH 1964/52b (newborn); s. 1050, cross-section, left side; Klüver-Barrera; x 32.

Anterior pole of promontory.

For key to numbered structures, see fig. VI-5.

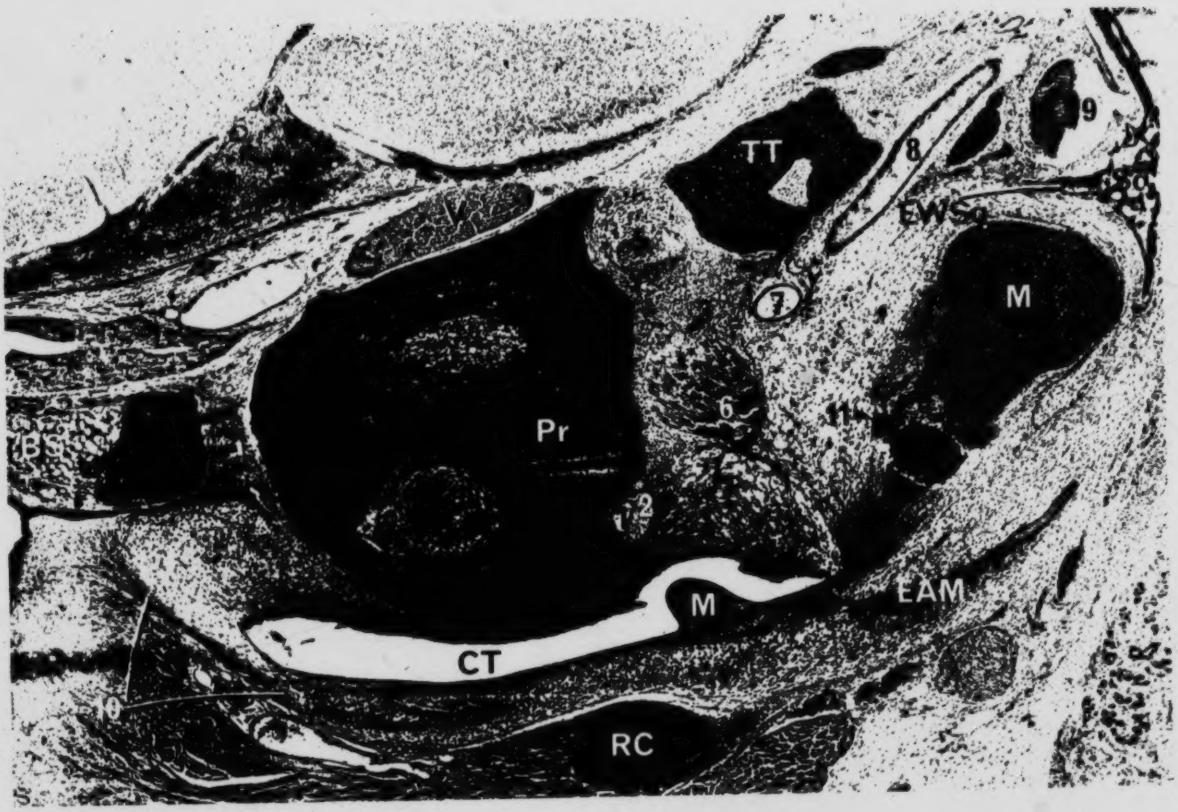

V
TT
8
9
EWS
7
M
6
11
Pr
BS
12
M
EAM
CT
10
RC

FIG. VI-7 E. europaeus MPIH 1964/52b (newborn); s. 1170, cross-section, right side (sides rev.); Klüver-Barrera; x 32.

Proximal portion of the ramus posterior of the stapedial a., near its origin.

1, internal carotid a.; 2, cavum tympani; 3, ramus posterior of the stapedial a.; 4, FMTC; 5, stapedius m.; 6, CTPP (lateral section); 7, posterior continuation of crista parotica.

FIG. VI-8 E. europaeus MPIH 1964/57 (4 days old); s. 1400, cross-section, left side; Klüver-Barrera; x 44.

Facial n. within foramen stylomastoideum primitivum. Note small ramus posterior of the stapedial a.

For key to numbered structures, see fig. VI-7.

FIG. VI-9 E. europaeus MPIH 1964/57 (4 days old); s. 1410, cross-section, left side; Klüver-Barrera; x 44.

This and the following figure illustrate the relationships of the medial and lateral ~~sections~~ of the caudal tympanic process of the petrosal to various structures.

For key to numbered structures, see fig. VI-7.

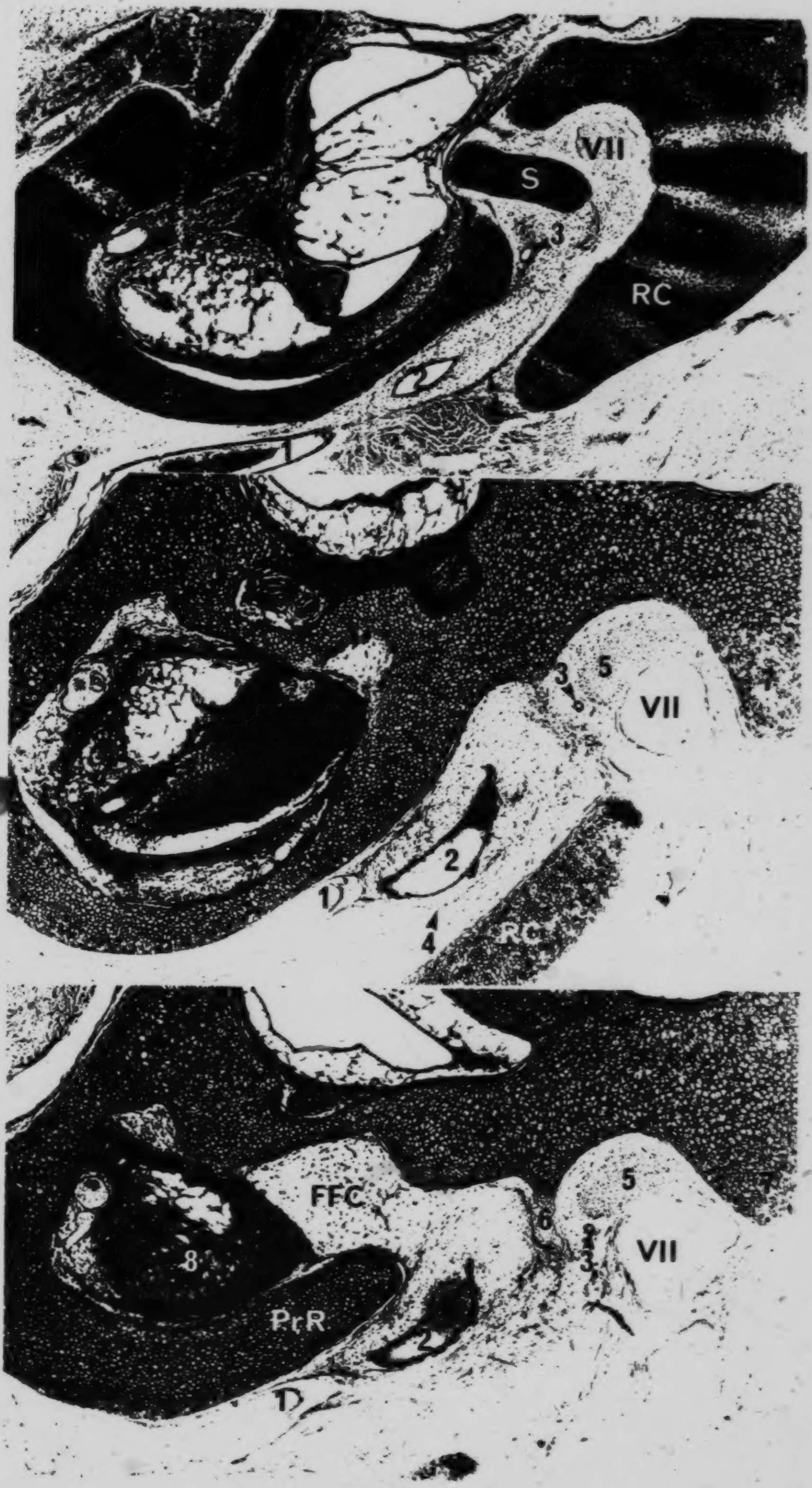

VII
S
3
RC
3
5
VII
2
1
4
RC
FFC
5
6
3
VII
8
PrR
2
1

FIG. VI-10 _E_. _europaeus_ MPIH 1964/57 (4 days old).

a. s. 1420, cross-section, left side; Klüver-Barrera; x 44.

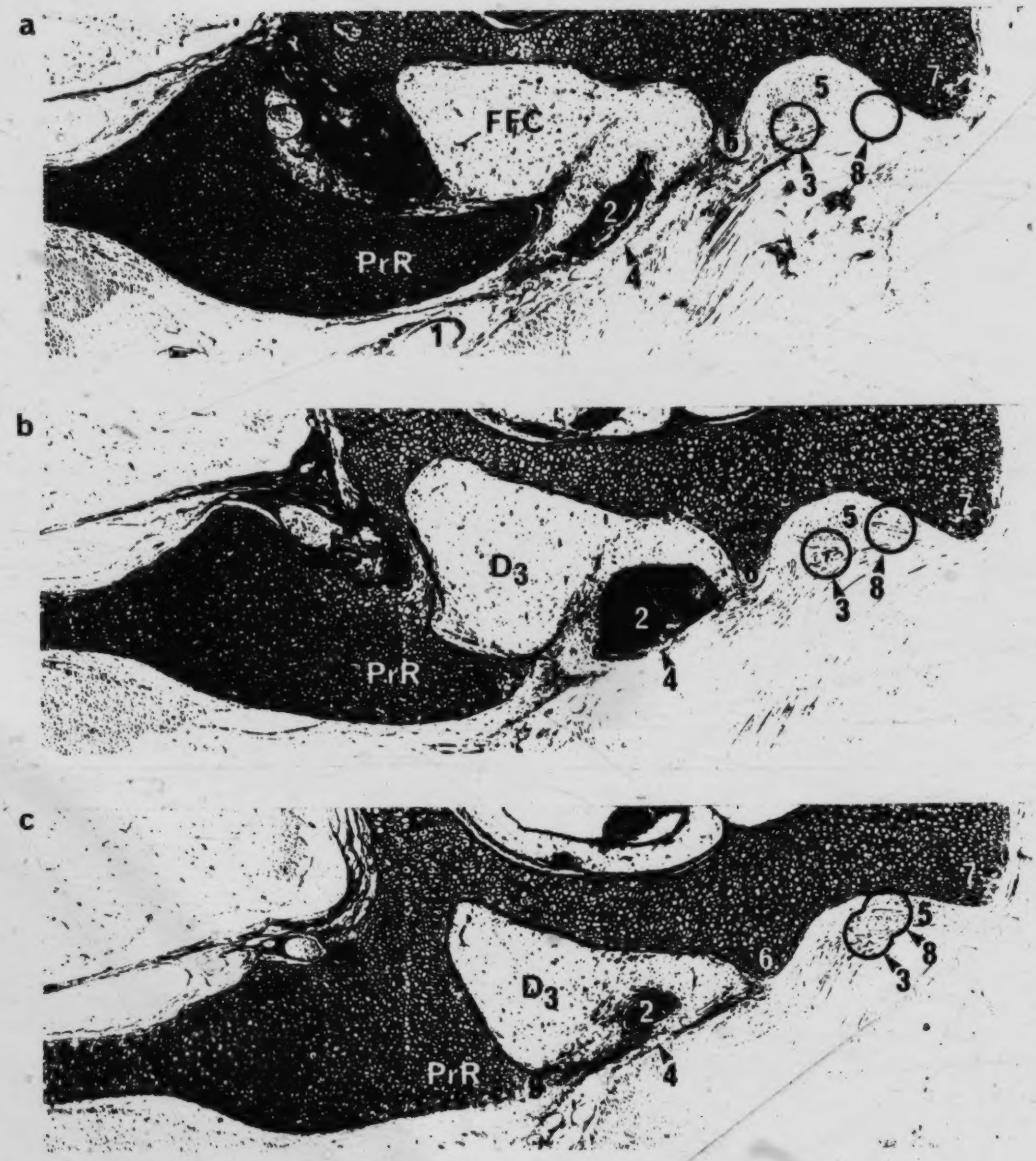
b. s. 1430, cross-section, left side; Klüver-Barrera; x 44.

c. s. 1440, cross-section, left side; Klüver-Barrera; x 44.

Series of sections through the medial and lateral sections of the caudal tympanic process of the petrosal. The lateral section is well-developed, but the medial section (which is a prolongation of the processus recessus) is barely indicated at this stage.

Also visible is ramus posterior of the stapedial a., distributing its terminal branches to the stapedius m. and its investing tissues. The ramus posterior cannot be traced beyond the level represented by fig. VI-10c.

1, internal carotid a.; 2, cavum tympani; 3, ramus posterior of stapedial a.; 4, FMTC; 5, stapedius m. in stapedius fossa; 6, CTPP (lateral section); 7, posterior continuation of crista parotica; 8, auricular ramus of vagus; 9, CTPP (medial section).


a
FFC
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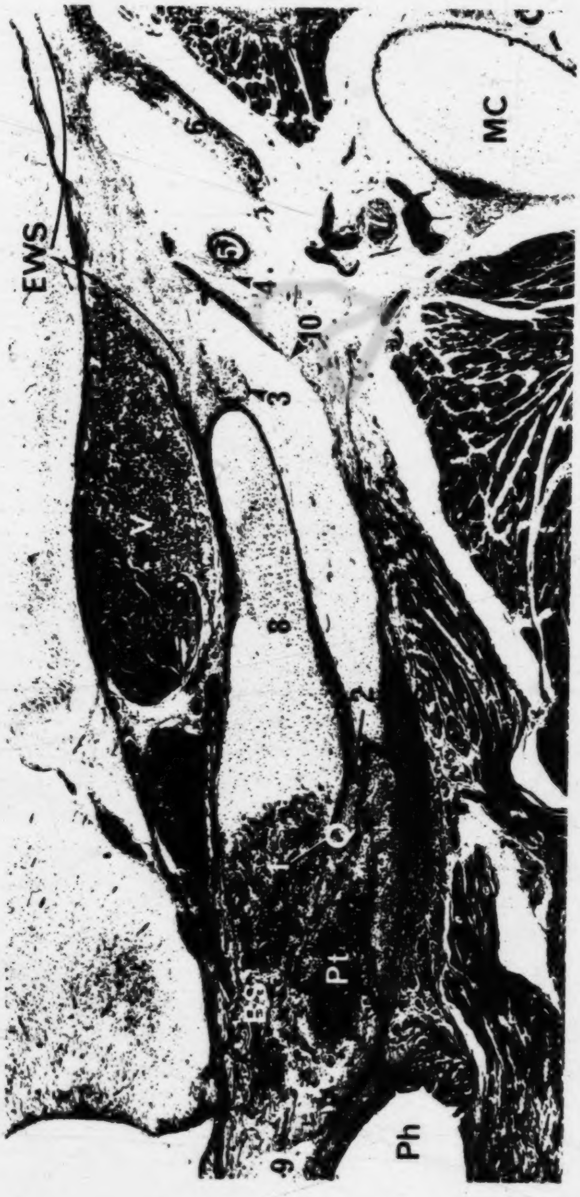
7
6
3
8
2
PrR
4
1
b
D3
5
7
6
8
3
2
4
PrR
c
7
5
8
3
6
D3
2
4
PrR

FIG. VI-11 *E. europaeus* MPIH 1966/146 (young infant); s. 1741, cross-section, right side (sides rev.); Azan; x 32.

Anterior end of presumptive tympanic cavity. The pterygoid is completely fused to the basisphenoid, but the pterygoid canal provides an anatomical boundary between the two.

1, artery of the pterygoid canal; 2, nerves of the pterygoid canal (entering pterygoid canal); 3, tensor tympani m.; 4, lesser petrosal n.; 5, ramus inferior of stapedial a.; 6, wall of sulcus for ramus inferior (part of tympanic process of alisphenoid); 7, chorda tympani; 8, processus alaris and ala temporalis; 9, basisphenoidal pit; 10, FMTC.


EWS
9
5
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10
3
MC
V
8
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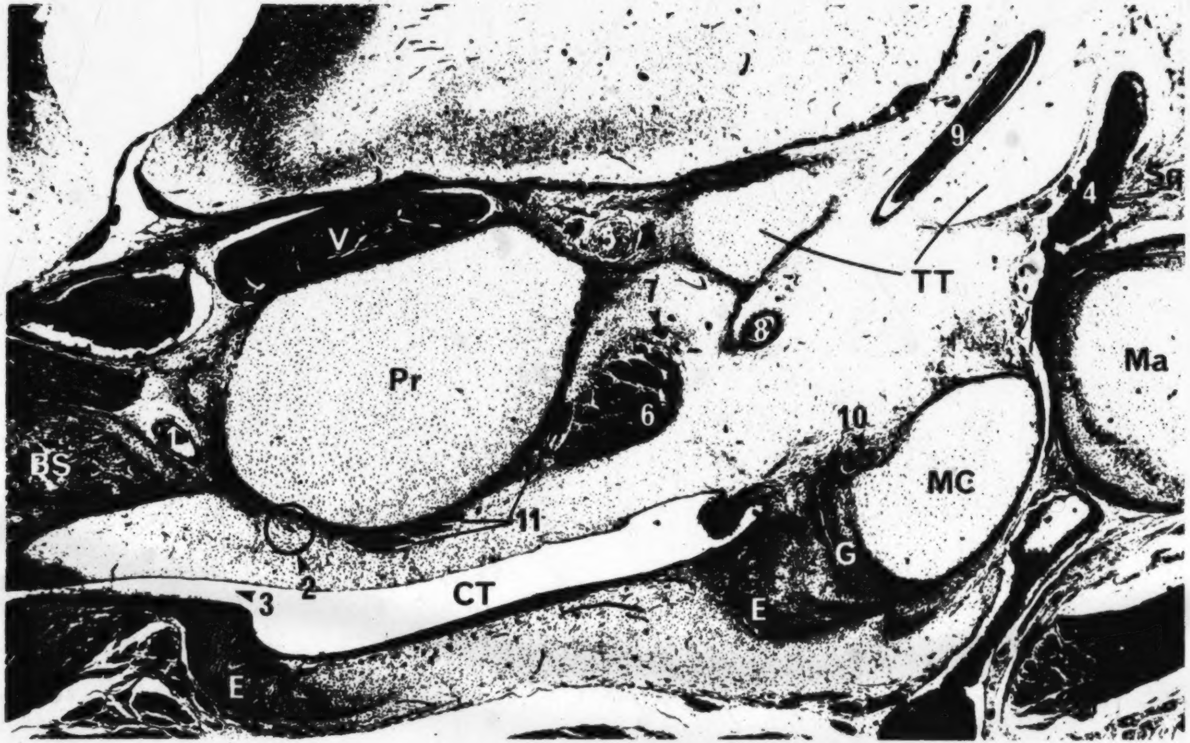
Bs
Pt
6
Ph

FIG. VI-12 E. europaeus MPIH 1966/146 (young infant); s. 1801, cross-section, right side (sides rev.); Azan; x 32.

Anterior pole of promontory and tegmen tympani.

1, promontorial a.; 2, artery of pterygoid canal; 3. lumen of auditory tube; 4, petrosquamous sinus; 5, geniculate ganglion; 6, tensor tympani; 7, lesser petrosal n.; 8, ramus inferior of stapedial a.; 9, ramus superior of stapedial a.; 10, chorda tympani; 11, tympanic plexus (greater petrosal and deep petrosal nn.).


9
4
Sa
V
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7
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MC
L
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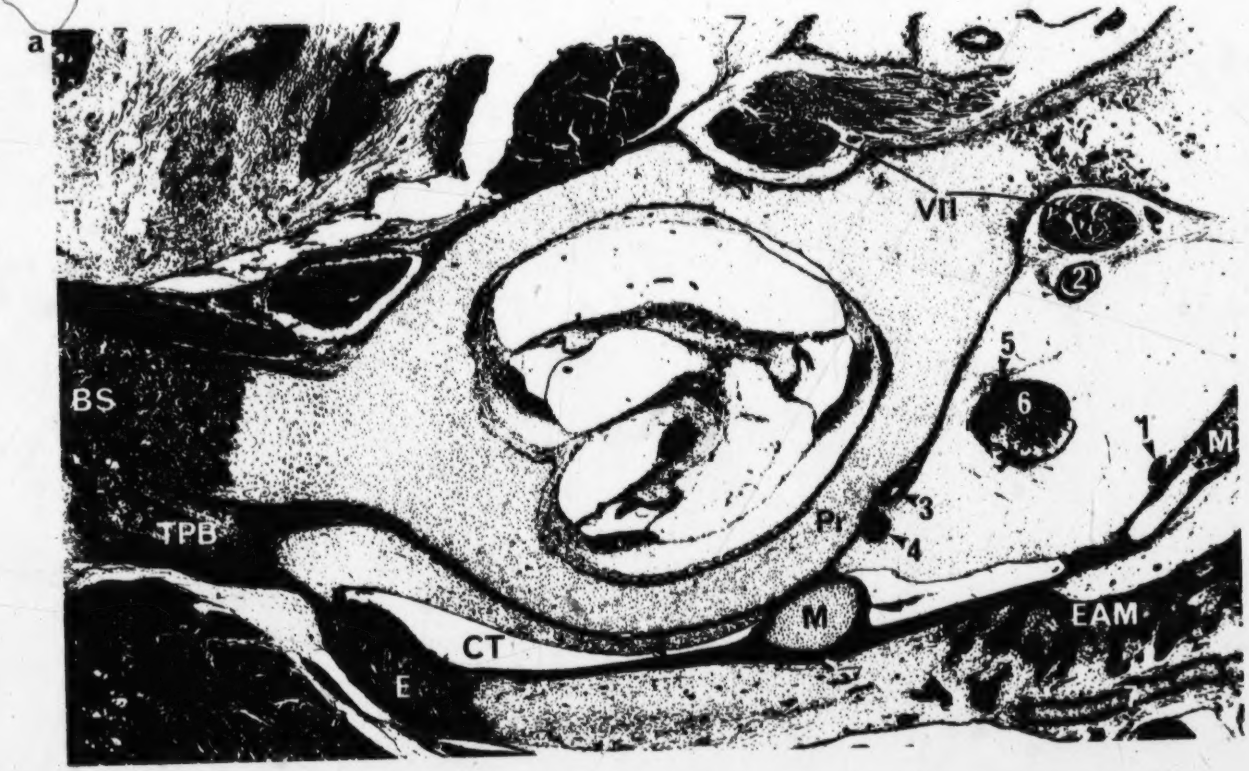
E
E

FIG. VI-13 E. europaeus MPIH 1966/146 (young infant); s. 1891, cross-section, right side (sides rev.); Azan.

a. Section through tympanic process of basisphenoid; x 32.

b. Enlargement of part of fig. VI-13a; x 108.

1, chorda tympani; 2, (proximal) stapedial a.; 3, internal carotid a.; 4, internal carotid n.; 5, lesser petrosal n.; 6, tensor tympani; 7, auricular cartilage.


a
VII
2
5
6
1
M
BS
TPB
Pr
3
4
M
EAM
CT
E

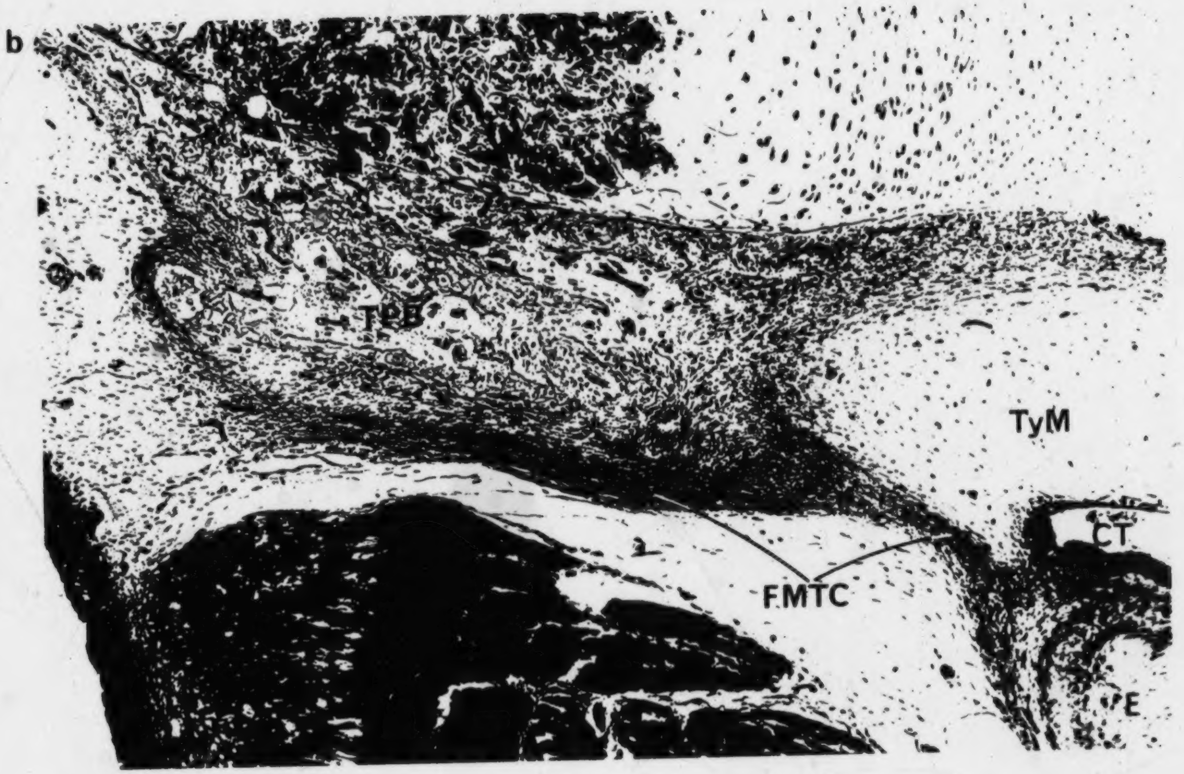

b
TpB
TyM
CT
FMTC
E

FIG. VI-14 *E. europaeus* MPIH 1966/146 (young infant); s. 1981, cross-section, left side; Azan; x 32.

Section illustrating massive size of crista parotica.

1, (proximal) stapedial a.; 2, internal carotid a.; 3, tendon of stapedius m.; 4, chorda tympani; 5, FMTC; 6, internal carotid n.; 7, external acoustic meatus; 8, anular ligament of stapes in fenestra vestibuli.

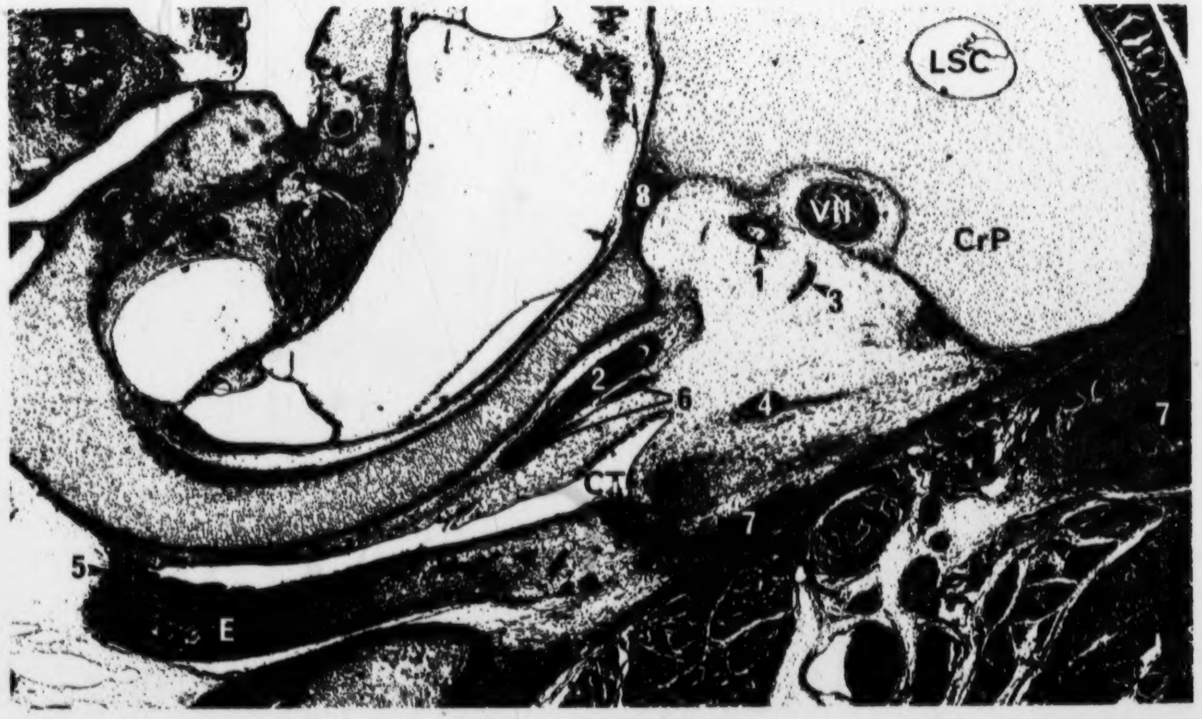

LSC
VII
CrP
8
1
3
2
6
4
7
CT
7
5
E

FIG. VI-15 *E. europaeus* MPIH 1966/146 (young infant); s. 1991, cross-section, left side; Azan; x 32.

This and the following three figures illustrate the relationships of the medial and lateral sections of the caudal tympanic process of the petrosal to various structures.

1, CTPP; 2, internal carotid a.; 3, tendon of stapedius m.; 4, chorda tympani; 5, FMTC; 6, internal carotid n.; 7, tympanic n. joining internal carotid n.

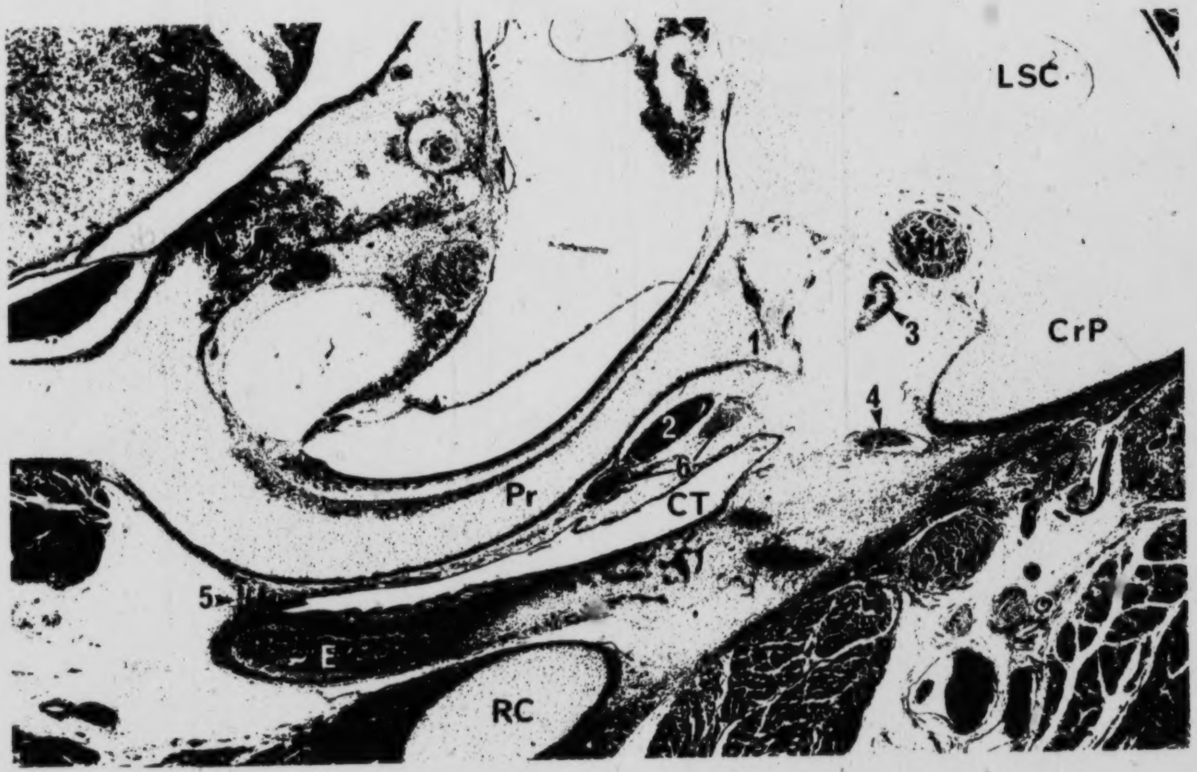

LSC
CrP
1
3
4
2
6
Pr
CT
5
E
RC

FIG. VI-16 E. europaeus MPIH 1966/146 (young infant); s. 2001, cross-section, left side; Azan; x 32.

Lateral section of caudal tympanic process of the petrosal.

For key to numbered structures, see fig. VI-15.

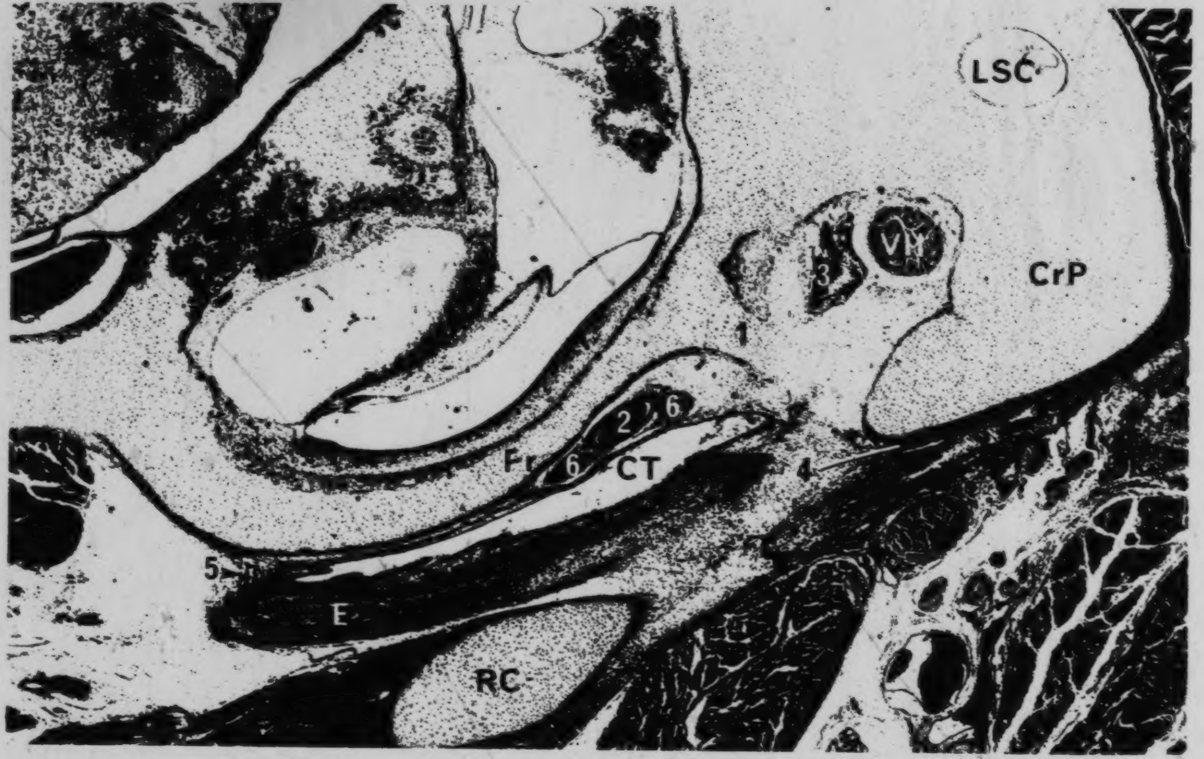

LSC
CrP
VII
3
1
2
6
F
6
CT
4
5
E
RC

FIG. VI-17 E. *europaeus* MPIH 1966/146 (young infant); s. 2011, cross-section, left side; Azan; x 32.

Lateral section of caudal tympanic process of the petrosal; the process almost meets Reichert's cartilage.

For key to numbered structures, see fig. VI-15.

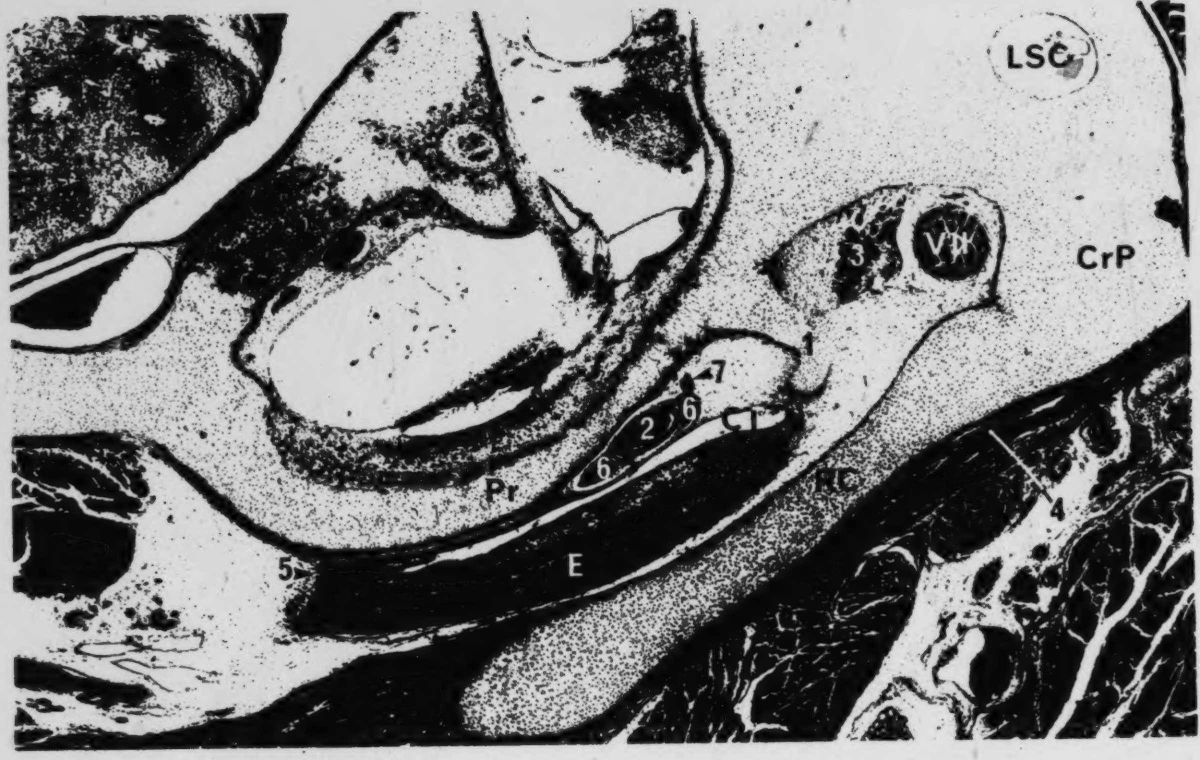

LSC
CrP
VII
3
1
7
6
2
6
CT
RC
4
Pr
E
5

FIG. VI-18 E. europaeus MPIH 1966/146 (young infant).

a. s. 2051, cross-section, left side; Azan; x 32.

b. s. 2071, cross-section, left side; Azan; x 32.

c. s. 2081, cross-section, left side; Azan; x 32.

Series of sections through the medial and lateral sections of the caudal tympanic process of the petrosal. The medial section is somewhat better-developed than in MPIH 1964/57 (cf. fig. VI-10), but it is still very small. The ramus posterior of the stapedial a. is represented only by a leash of small vessels beneath the stapedius m. (asterisks).

1, stapedius m.; 2, posterior continuation of crista parotica; 3, auricular ramus of the vagus n.; 4, internal carotid a.; 5, internal carotid n.; 6, tympanic n.; 7, CTPP (lateral section); 8, FMTC; 9, CTPP (medial section).

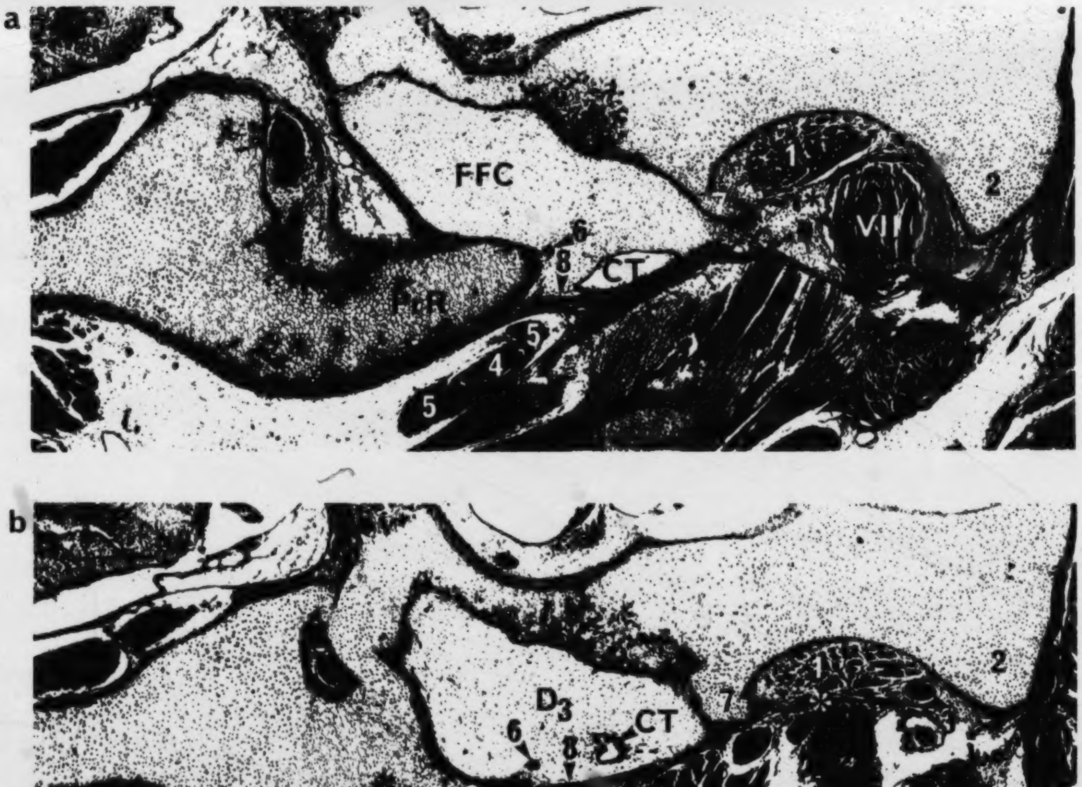
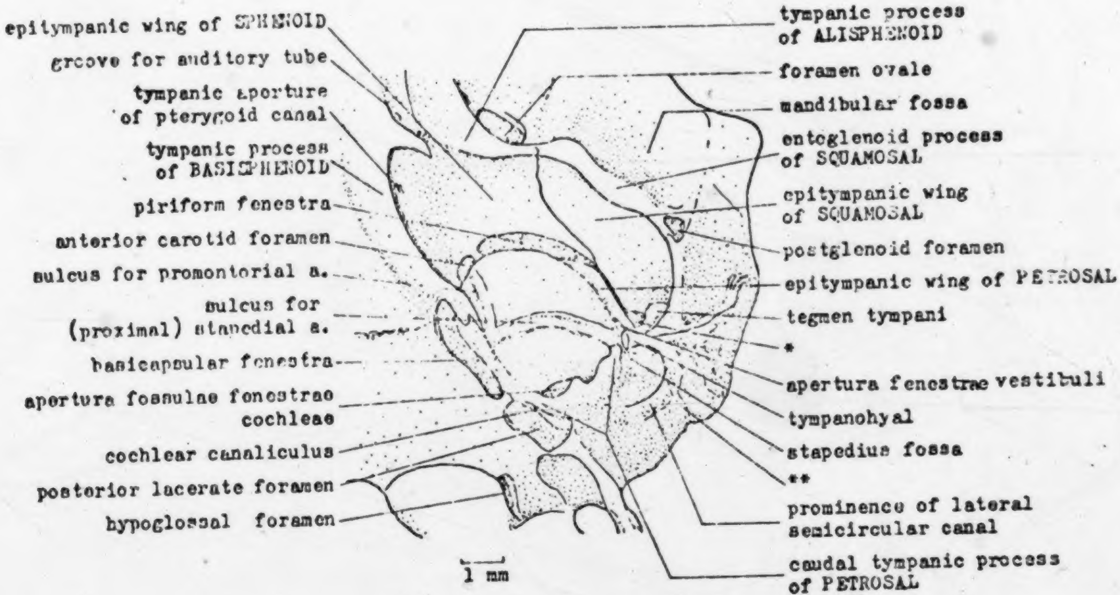
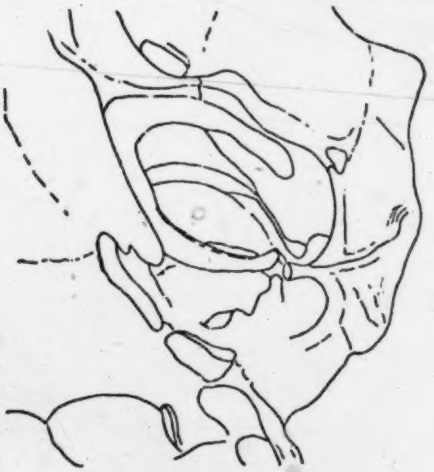

a
FFC
1
2
VII
6
8
CT
FR
5
4
5
b
D$_3$
CT
6
8
7
1
2
VII
9
5
4
c
D$_3$
6
7
2
3
9
8
4

FIG. VII-1 *M. dobsoni* adult. General view of left auditory region, ventral aspect.

In the upper figure, the ectotympanic and parts of the tympanic process of the basisphenoid and caudal tympanic process of the petrosal have been removed in order to expose hidden structural details. In the middle figure, all bones and processes are depicted as complete and *in situ*. The dashed line represents the boundary between the actual ventral surface of the promontory and the outgrowths arising from it. The low ridge extending along the medial side of the promontory may be a rostral tympanic process of the petrosal. The apertura fossulae fenestrae cochleae and diverticulum D_3 are hidden in both figures by the large caudal tympanic process of the petrosal.

The lower figure depicts the tympanic branchings of the carotid system.


epitympanic wing of SPHENOID
groove for auditory tube
tympanic aperture of pterygoid canal
tympanic process of BASISPHENOID
piriform fenestra
anterior carotid foramen
sulcus for promontorial a.
sulcus for (proximal) stapedial a.
basicapsular fenestra
apertura fossulae fenestrae cochleae
cochlear canaliculus
posterior lacerate foramen
hypoglossal foramen
1 mm
tympanic process of ALISPHENOID
foramen ovale
mandibular fossa
entoglenoid process of SQUAMOSAL
epitympanic wing of SQUAMOSAL
postglenoid foramen
epitympanic wing of PETROSAL
tegmen tympani
*
apertura fenestrae vestibuli
tympanohyal
stapedius fossa
**
prominence of lateral semicircular canal
caudal tympanic process of PETROSAL



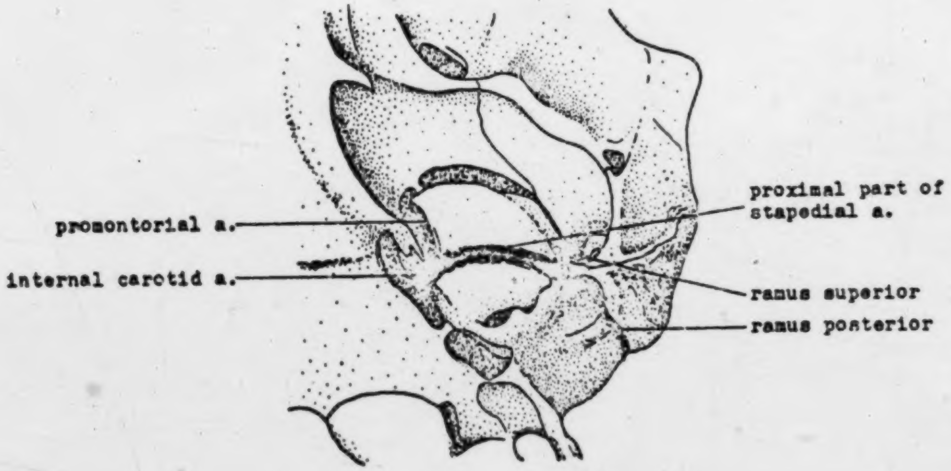
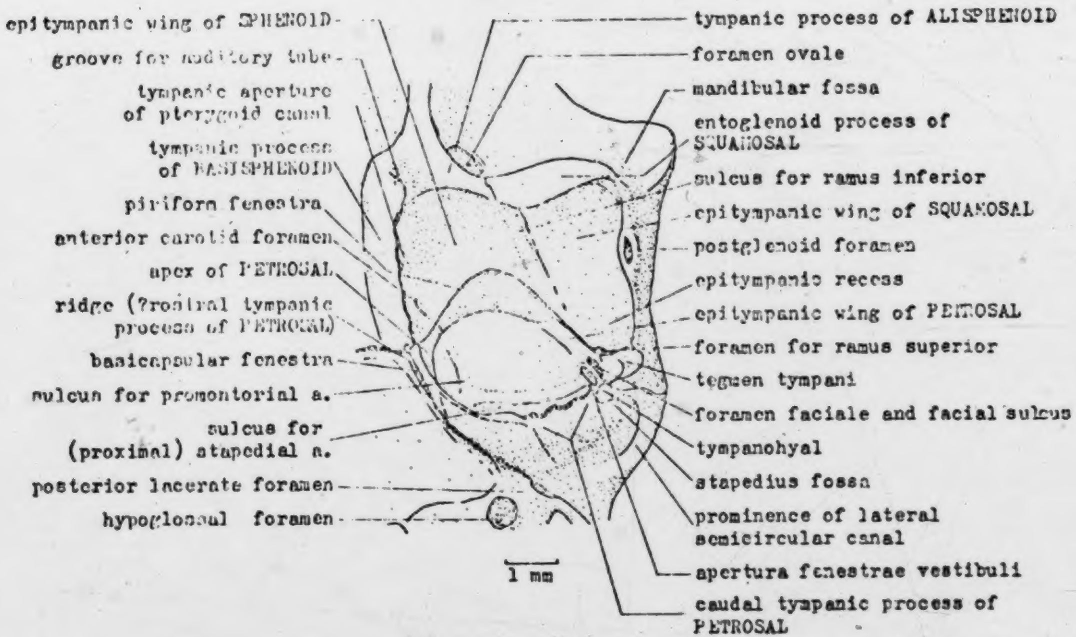

promontorial a.
internal carotid a.
proximal part of stapedial a.
ramus superior
ramus posterior

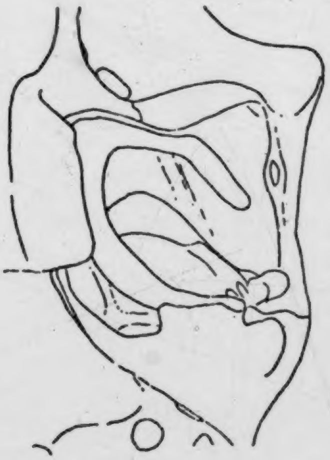
FIG. VII-2 H. semispinosus adult. General view of left auditory region, ventral aspect.

In the upper figure, the ectotympanic and part of the tympanic process of the basisphenoid have been removed in order to expose hidden structural details. The middle figure represents the auditory region prior to dissection. Obvious differences from M. dobsoni (see fig. VII-1) include a smaller caudal tympanic process of the petrosal which does not contact the ectotympanic, isolation of the anterior carotid foramen within the epitympanic wing of the sphenoid, a sulcus for the inferior ramus of the stapedial artery (latter artery not present in M. dobsoni), absence of a medial ridge on the ventral surface of the promontory, and a relatively larger basicapsular fenestra and posterior lacerate foramen.

The lower figure depicts the tympanic branchings of the carotid system.

*, foramen for the ramus superior of the stapedial a., into which the foramen faciale opens; **, groove on mastoid, possibly for ramus posterior of stapedial a.


epitympanic wing of SPHENOID
groove for auditory tube
tympanic aperture of pterygoid canal
tympanic process of BASISPHENOID
piriform fenestra
anterior carotid foramen
apex of PETROSAL
ridge (?rostral tympanic process of PETROSAL)
basicapsular fenestra
sulcus for promontorial a.
sulcus for (proximal) stapedial a.
posterior lacerate foramen
hypoglossal foramen
1 mm
tympanic process of ALISPHENOID
foramen ovale
mandibular fossa
entoglenoid process of SQUAMOSAL
sulcus for ramus inferior
epitympanic wing of SQUAMOSAL
postglenoid foramen
epitympanic recess
epitympanic wing of PETROSAL
foramen for ramus superior
tegmen tympani
foramen faciale and facial sulcus
tympanohyal
stapedius fossa
prominence of lateral semicircular canal
apertura fenestrae vestibuli
caudal tympanic process of PETROSAL



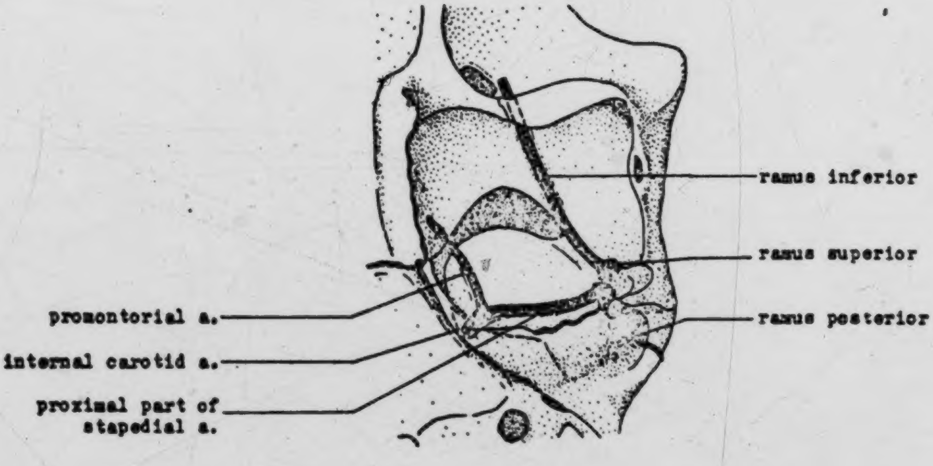

ramus inferior
ramus superior
ramus posterior
promontorial a.
internal carotid a.
proximal part of stapedial a.

FIG. VII-3 Right auditory regions of some tenrecoids (after MCDOWELL 1958). Not to same scale. A, Potamogale velox; B, Limnogale mergulus; C, Microgale (Nesogale) sp.; D, Geogale aurita; E. Echinops telfairi; F, Tenrec ecaudatus; G, Hemicentetes semispinosus.

AC

AC, alisphenoid canal; AV, cochlear canaliculus; CF, posterior carotid foramen or incisure; EF, ethmoidal foramen; EH, tympanohyal; ETR, epitympanic recess; FLA, foramen lacerum anterius (sphenorbital fissure); FLP, foramen lacerum posterius; FPM, anterior process of malleus; FR, apertura fossulae fenestrae cochleae; FSA foramen for ramus superior of stapedial artery; FSM, fossa for stapedius muscle; GCT, groove for chorda tympani; GF, mandibular fossa; HF, hypoglossal foramen; HSC, lateral semicircular canal; IPS, persistent basicapsular fenestra; MA, malleus; NF, foramen for persistent notochord; OF, foramen ovale; PGF, postglenoid foramen; PGP, postglenoid process; PH, hamular process of pterygoid; PP, paroccipital process; PY, persistent piriform fenestra; RI, foramen for ramus inferior and lesser petrosal nerve (or latter only); SMF, foramen stylomastoideum; TP, caudal tympanic process of petrosal; TY, ectotympanic; TYB, tympanic process of basisphenoid or vestige of same.

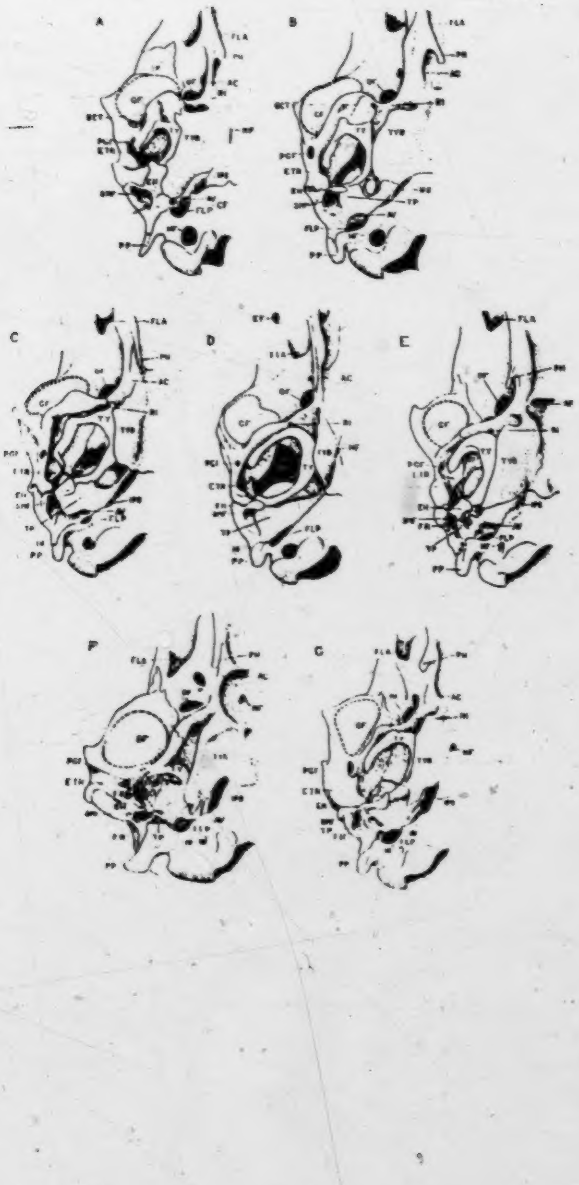
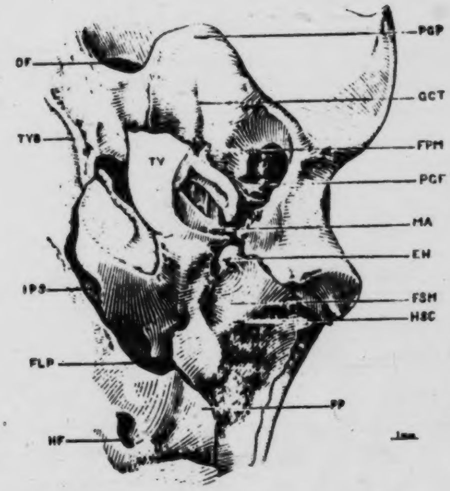
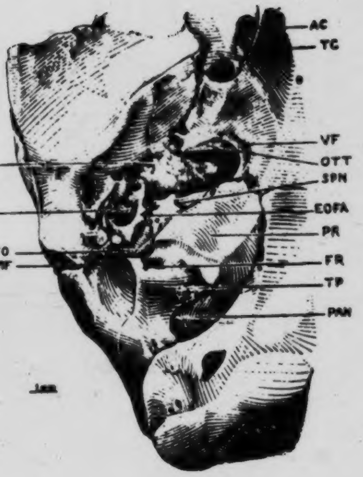

A
FLA
AC
GF
BCT
ETR
TYB
TT
EH
CF
FLP
PP
B
FLA
AC
BCT
CF
TT
TYB
PCF
ETR
EH
TP
FLP
PP
C
FLA
AC
CF
PCF
TYB
TP
PP
D
FLA
AC
PCF
CTR
TP
FLP
PP
E
FLA
PCF
TYB
EH
PP
F
FLA
PCF
ETR
TP
PP
G
FLA
AC
PCF
CTR
TYB
EH
TP
PP

FIG. VII-4 Ventral views of auditory region of Solenodon paradoxus (after MCDOWELL 1958). A, juvenile, with ectotympanic removed; B, adult; C, tympanic branchings of carotid.

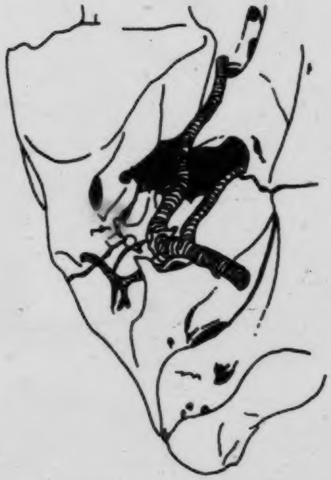
AP, promontorial artery; AS, proximal part of stapedial artery; EOFA, foramen faciale; FO, apertura fenestrae vestibuli; ICA, internal carotid artery; OTT, alisphenoid origin of tensor tympani muscle; PAN, passage for auricular ramus of vagus nerve; PR, promontory; RI, ramus inferior of stapedial artery; RP, ramus posterior of stapedial artery; RS, ramus superior of stapedial artery; SPN, foramen for greater petrosal nerve; ST, stapes; TC, transverse canal; VF, tympanic aperture of pterygoid canal. (For key to other named structures, see fig. VIII-3).


PGP
DF
GCT
TYB
TV
FPM
PGF
MA
EM
IPS
FSM
HSC
FLP
PP
HF
1mm

A


AC
TC
VF
OTT
PY
SPN
ETR
EOFA
PR
FO
SMF
FR
TP
PAN
1mm

B



C

FIG. VII-5 *H. semispinosus* MPIH 1964/84 (fetus); s. 842, cross-section, left side; Klüver-Barrera; x 47.

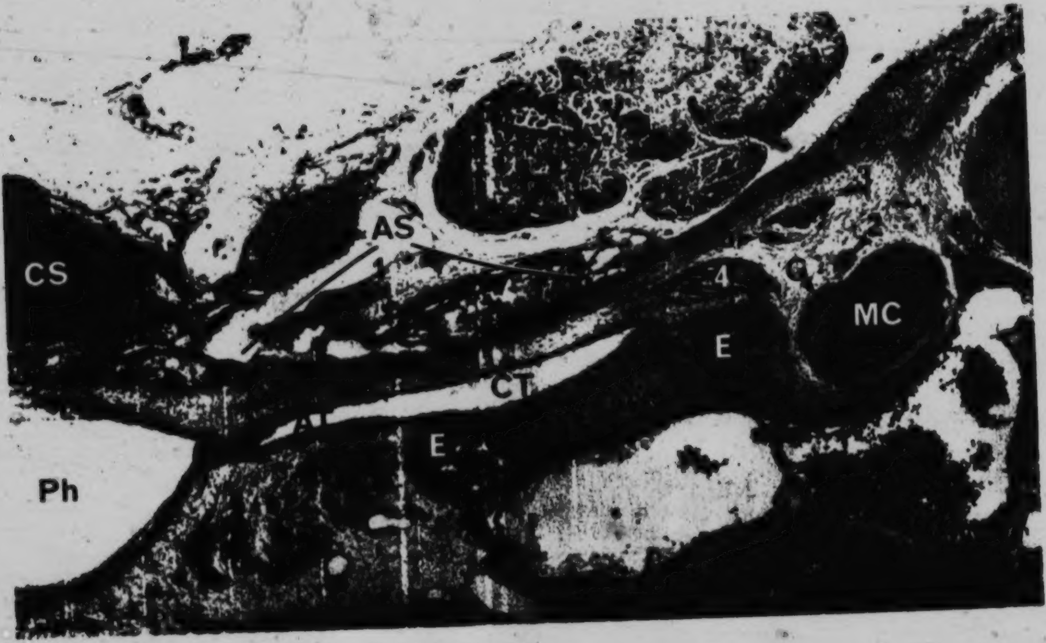
Section through tympanic aperture of auditory tube.

1, nerves of the pterygoid canal; 2, chorda tympani; 3, otic ganglion; 4, tensor veli palatini m.; 5, lesser petrosal n. (to otic ganglion).

FIG. VII-6 *H. semispinosus* MPIH 1964/84 (fetus); s. 912, cross-section, left side; Klüver-Barrera; x 47.

Section through mid-part of pars cochlearis. The epitympanic wings of the petrosal and squamosal are both present, but are separated by a wide interval at this stage (posterior section of piriform fenestra).

1, external acoustic meatus; 2, greater petrosal n.; 3, lesser petrosal n.; 4, tensor tympani; 5, chorda tympani; 6, ramus superior of stapedial a. (middle meningeal a.); 7, promontorial a. and internal carotid n.; 8, petrosquamous sinus; 9, FMTC.


AS
1
CS
4
6
MC
E
CT
E
Ph

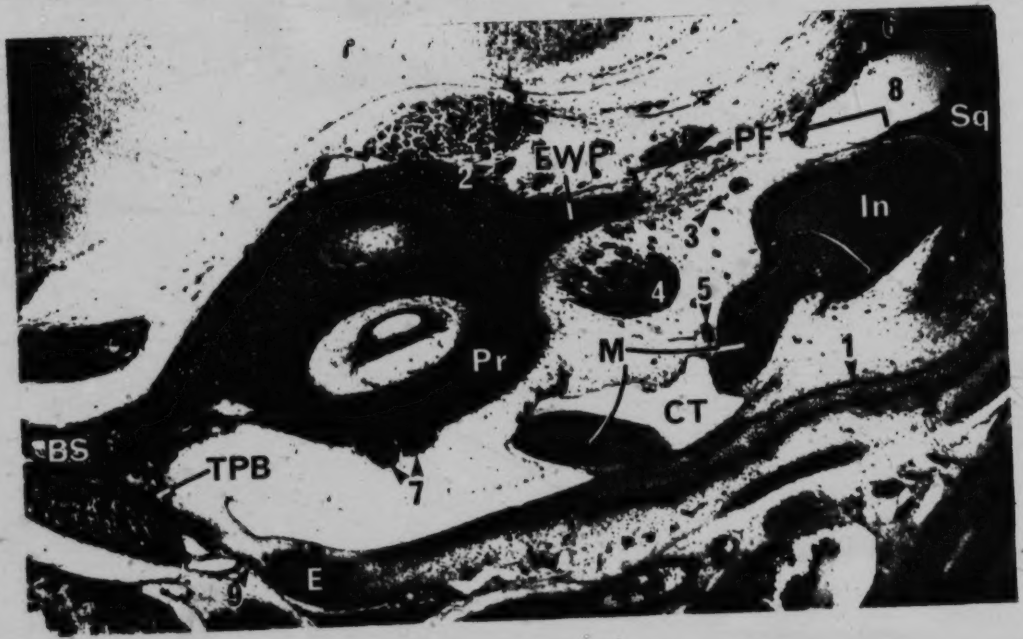

8
Sq
PF
EWP
2
In
3
4
5
M
Pr
CT
1
BS
TPB
7
9
E

FIG. VII-7 H. semispinosus MPIH 1964/84 (fetus).

a. s. 982, cross-section, right side (sides rev.); Klüver-Barrera; x 47.

b. s. 992, cross-section, right side (sides rev.); Klüver-Barrera; x 47.

c. s. 1012, cross-section, right side (sides rev.); Klüver-Barrera; x 47.

The lateral section of the caudal tympanic process of the petrosal, in the adult, extends anteriorly as far as the sulcus for the (proximal) stapedial a. In this young specimen, this part of the process is barely distinguishable as a low cartilaginous ridge on the rear of the pars cochlearis (asterisks). Note that the internal carotid a. bifurcates as soon as it enters the presumptive tympanic cavity.

1, stapedial a. (proximal portion); 2, promontorial a.; 3, ramus posterior of the stapedial a.; 5, stapedius m.; 6, tympanic n.; 7, FMTC; 8, chorda tympani; 9, posterior continuation of crista parotica; 10, internal carotid n.

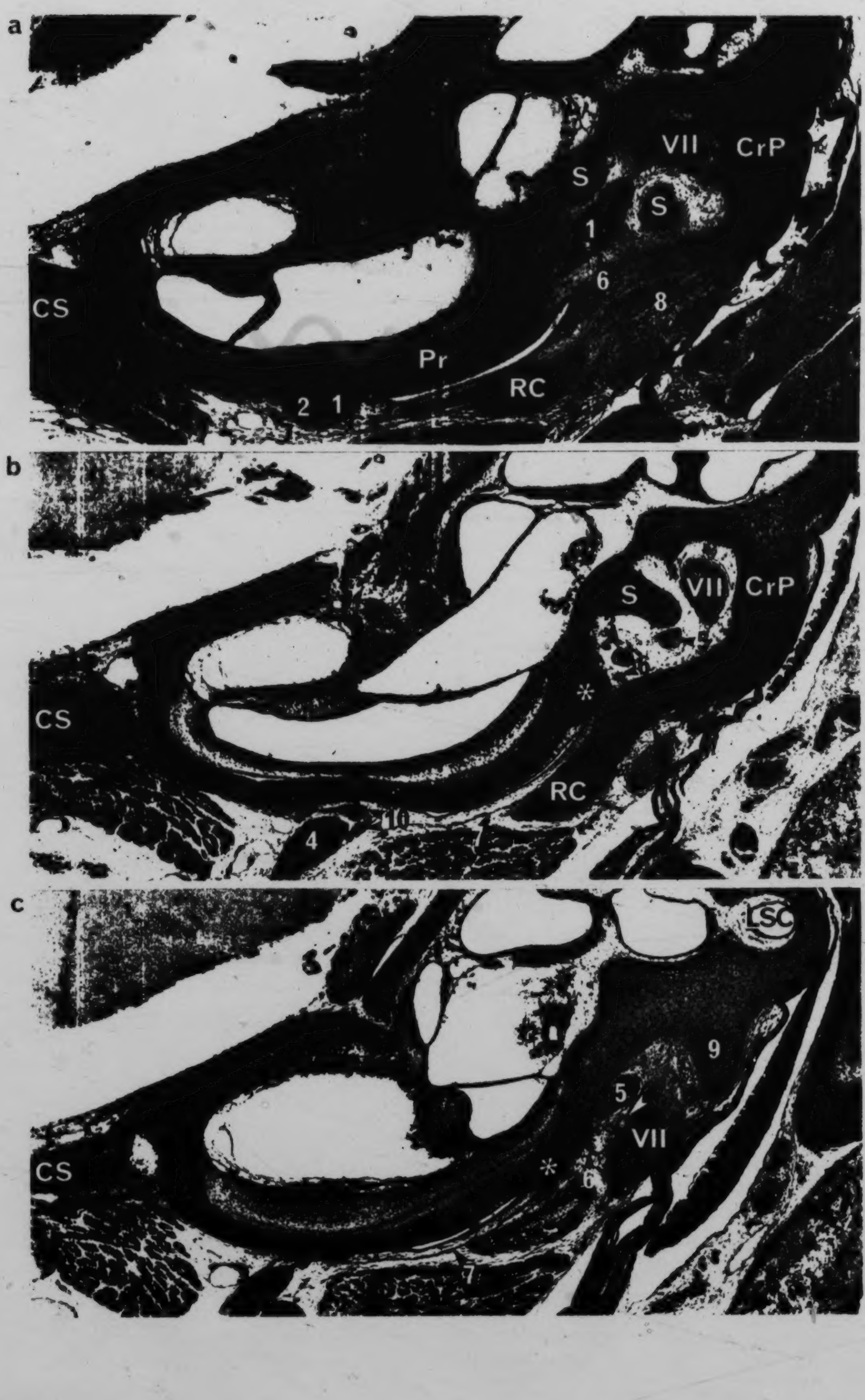

a
VII
CrP
S
S
1
6
8
CS
Pr
RC
2
1
b
S
VII
CrP
*
CS
RC
4
10
7
c
LSC
9
5
VII
CS
*
6
7

FIG. VII-8 *H. semispinosus* MPIH 1964/84 (fetus).

a. s. 1022, cross-section, right side (sides rev.); Klüver-Barrera; x 47.

b. s. 1032, cross-section, right side (sides rev.); Klüver-Barrera; x 47.

c. s. 1052, cross-section, right side (sides rev.); Klüver-Barrera; x 47.

From its origin behind the sulcus for the (proximal) stapedial a., the lateral section of the CTPP (asterisks) extends along the posterior pole of the promontory and terminates on the anteroventral surface of the pars canalicularis. The processus recessus posterior has not yet formed.

1, perilymphatic duct; 2, ramus posterior of the stapedial a.; 3, posterior continuation of the crista parotica; 4, stapedius m.; 5, FMTC; 6, internal jugular v.; 7, secondary tympanic membrane; 8, auricular ramus of the vagus; 9, tympanic n.

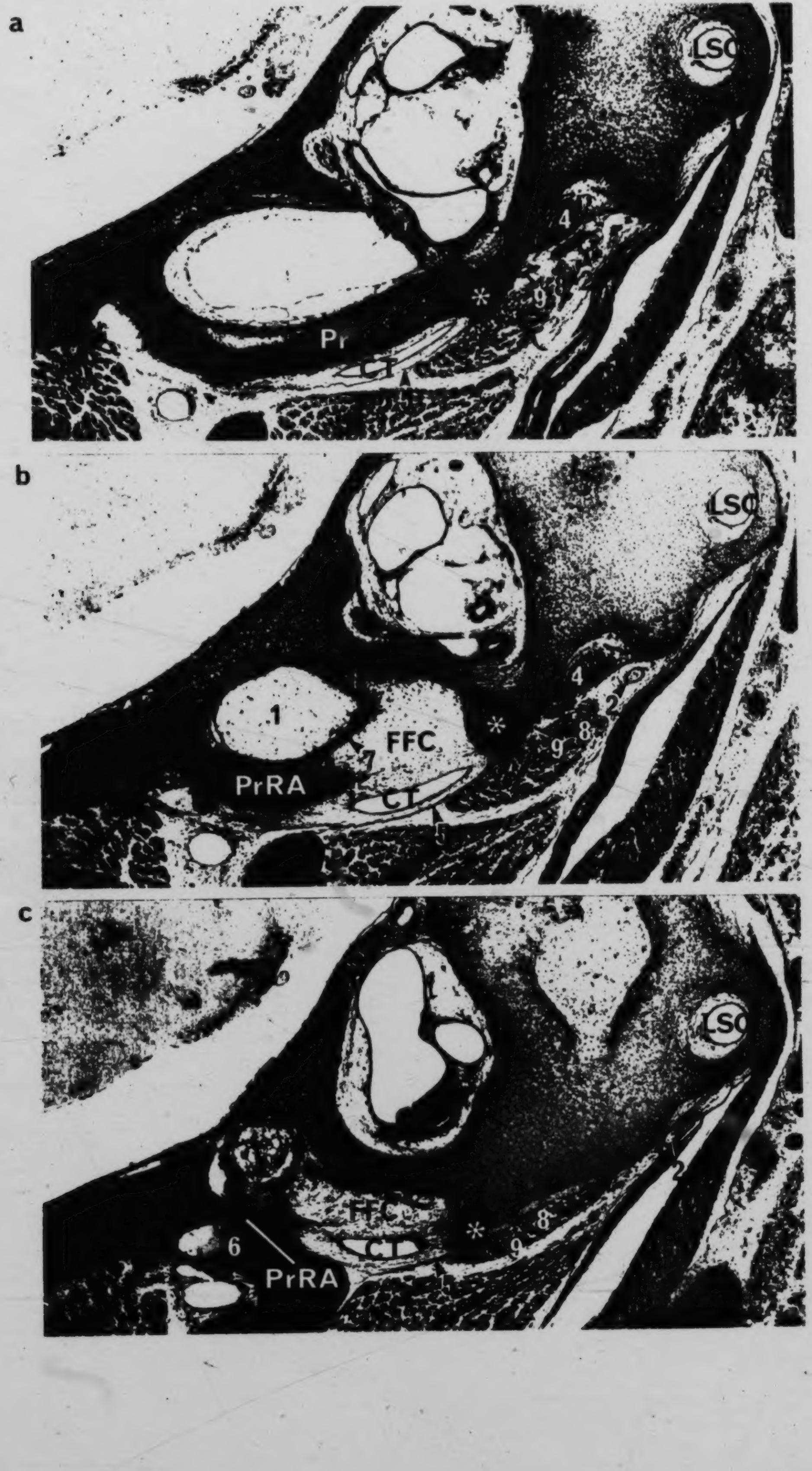

a
LSC
4
*
9
Pr
CT
b
LSC
4
2
8
9
*
1
FFC
7
PrRA
CT
c
LSC
2
FFC
*
8
9
CT
6
PrRA

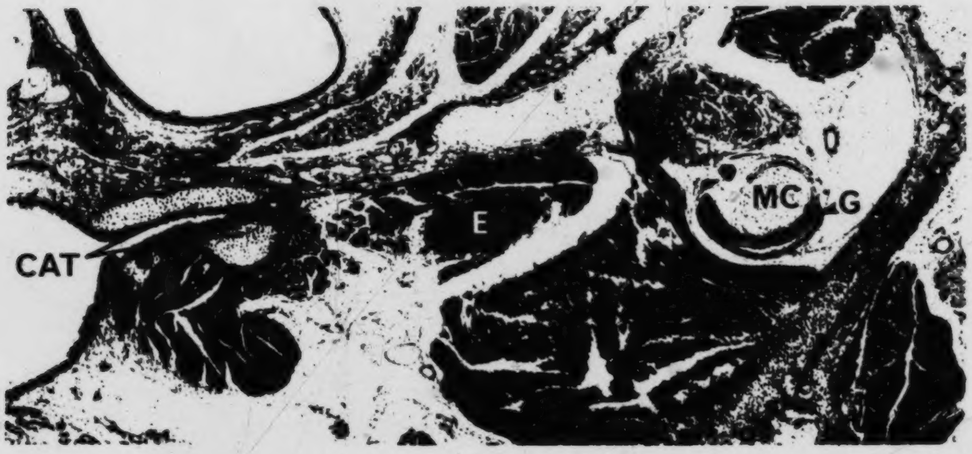
FIG. VII-9 *H. semispinosus* MPIH 1964/45 (near-term fetus); s. 1312, left side; Azan; x 36.

Section through cartilage of the auditory tube. There is no sign of an entotympanic element.

FIG. VII-10 *H. semispinosus* MPIH 1964/45 (near-term fetus); s. 1332, cross-section, left side; Azan; x 36.

Section through anterior end of presumptive tympanic cavity. The greatly-thickened body of the alisphenoid (asterisk) represents the developing tympanic process of the alisphenoid, although this is not particularly evident because of the transverse plane of sectioning. Since the nerves of the pterygoid canal enter the substance of the alisphenoid even at this stage, the position of the tympanic aperture of the canal is no guide to the approximate location of the pterygoid element (which is fused to the sphenoid in any event).

1, nerves of the pterygoid canal; 2, lesser petrosal n.; 3, tensor veli palatini m.; 4, chorda tympani, 5, FMTC.


CAT
E
MC
G

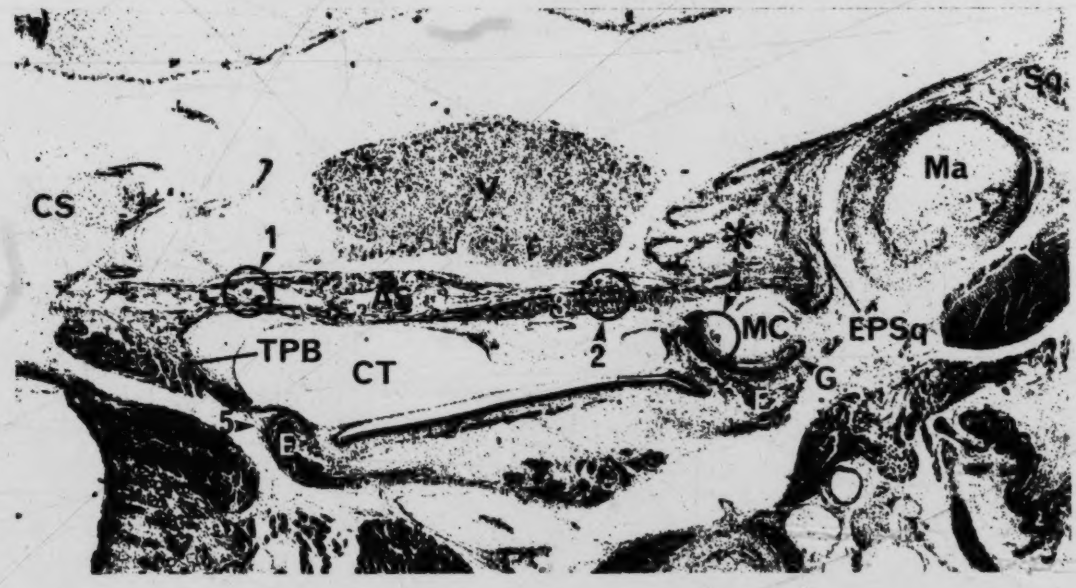

Sq
Ma
CS
V
1
AS
*
MC
EPSq
2
TPB
CT
G
F
5
E

FIG. VII-11 _H_. _semispinosus_ MPIH 1964/45 (near-term fetus); s. 1352, cross-section, left side; Azan.

a. Section through tympanic process of basisphenoid; x 47.

b. Enlargement of area around tympanic process of basisphenoid, showing relationship of latter to the FMTC. Note that the ventral end of the process is actively growing, as indicated by the presence of numerous osteoblasts. However, the relationship between the tympanic process of the basisphenoid and the ectotympanic is still athictic (and not semiphaneric, as in the adult stage); x 108.

1, promontorial a. (cerebral carotid a.) joining circulus arteriosus; 2, tensor veli palatini; 3, chorda tympani; 4, lesser petrosal n.; 5, cavernous sinus; 6, nerves of the pterygoid canal.

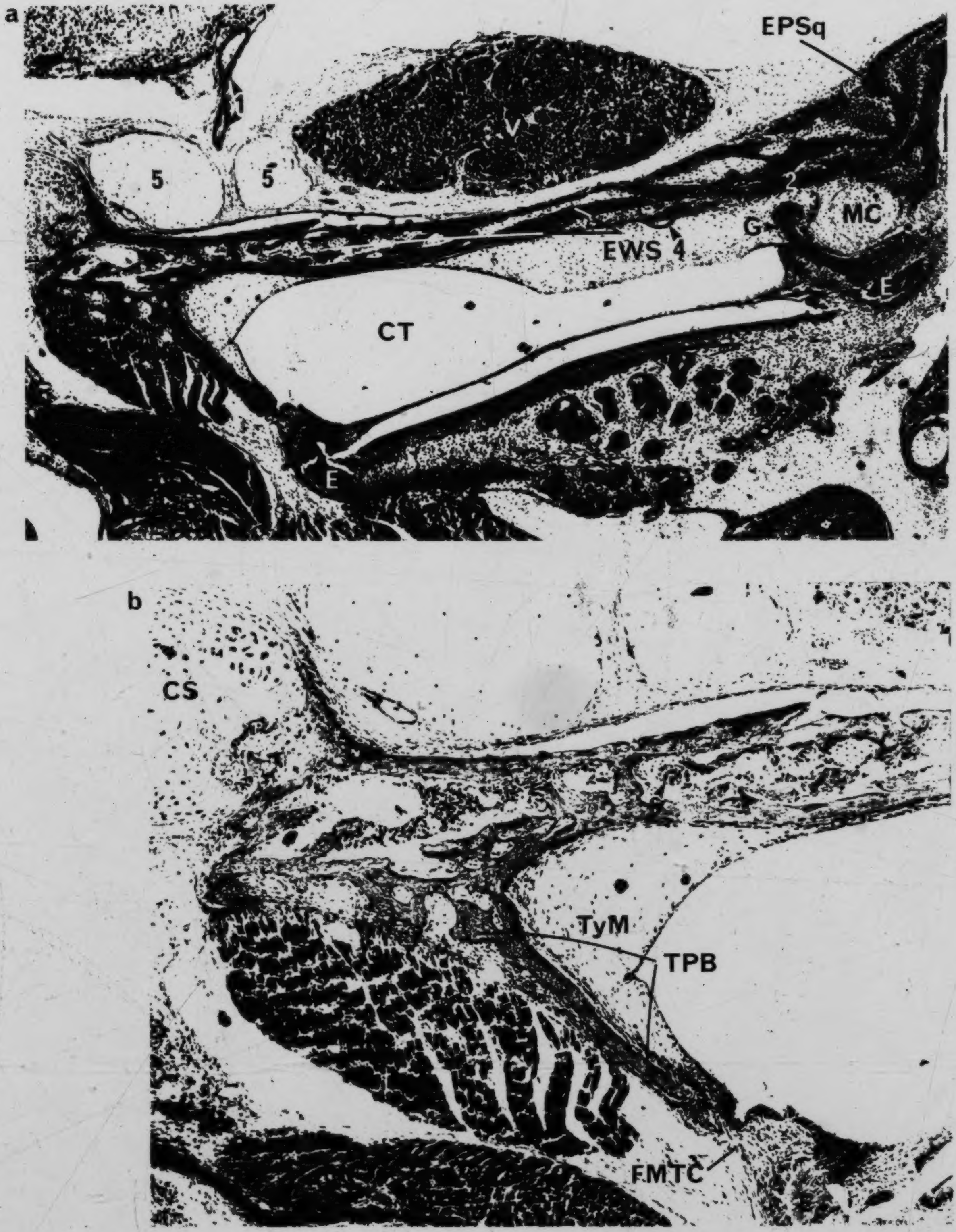

a
EPSq
5
5
V
2
MC
G
EWS
4
E
CT
E
b
CS
TyM
TPB
FMTC

FIG. VII-12 H. semispinosus MPIH 1964/45 (near-term fetus); s. 1452, cross-section, Azan; x 31.

Processes of the basisphenoid precociously develop around the degenerating alicochlear commissures, thus defining the definitive anterior carotid foramen.

1, tensor tympani m.; 2, internal carotid n.; 3, promontorial a.; 4, alicochlear commissure (degenerating); 5, processes of basisphenoid surrounding commissures; 6, chorda tympani; 7, anterior basicapsular commissure; 8, lesser petrosal n.; 9, FMTC.

FIG. VII-13 H. semispinosus MPIH 1964/45 (near-term fetus); s. 1462, cross-section, right side; Azan; x 36.

The basisphenoid also sends out processes to enclose the degenerating anterior basicapsular commissure (7), thus completing the rear wall of the anterior carotid foramen.

For key to numbered structures, see fig. VII-12.

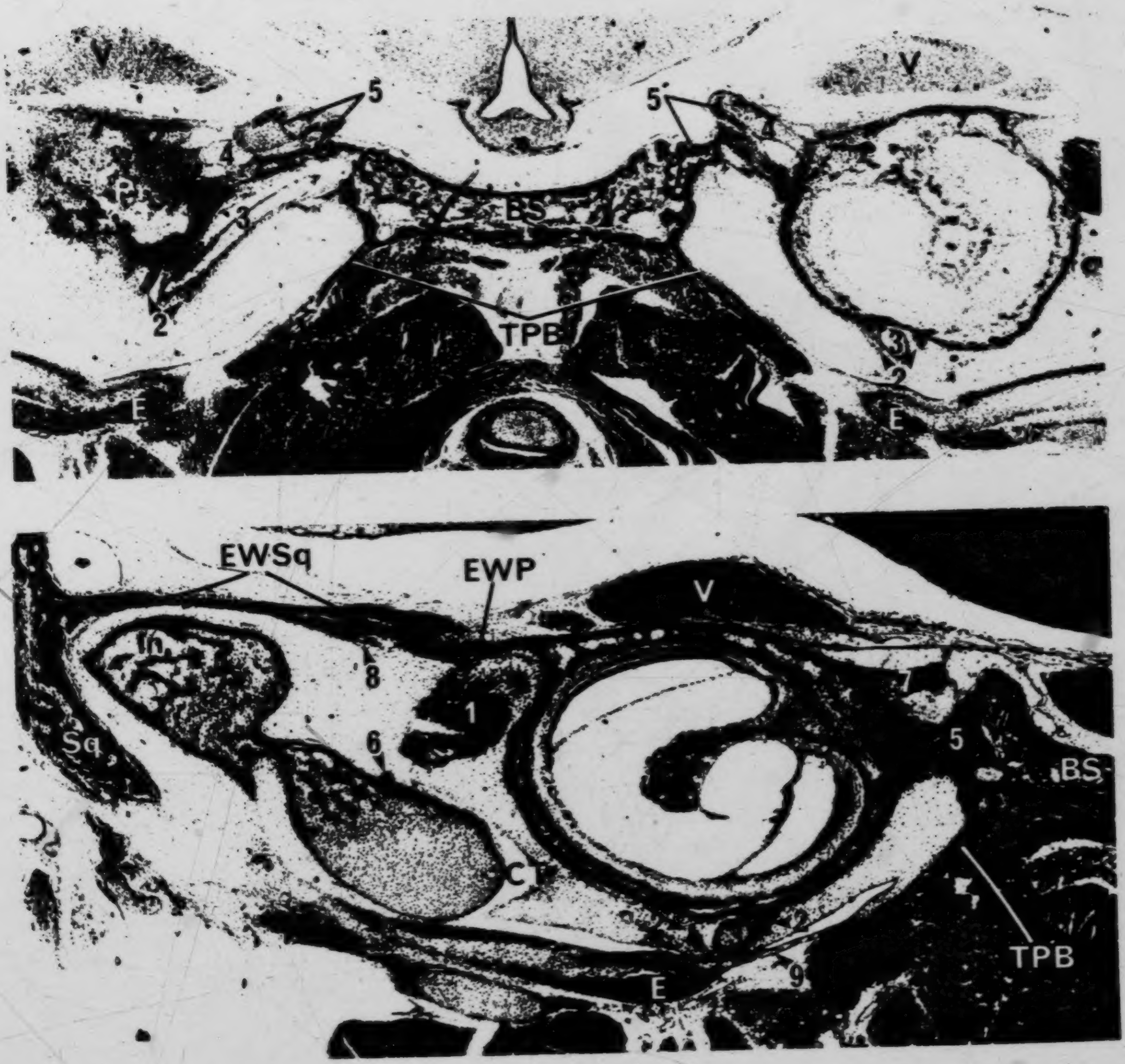

V
V
5
5
4
P
3
2
BS
TPB
3
2
E
E
EWSq
EWP
V
In
8
1
6
7
5
BS
Sq
CT
TPB
9
E

FIG. VII-14 *H. semispinosus* MPIH 1964/45 (near-term fetus); s. 1502, cross-section, right side; Azan; x 42.

The piriform fenestra extends to the posterolateral end of the dorsal wall, due to the insignificant development of the tegmen tympani. This section passes through the terminal part of the fenestra, which serves as the aperture through which the ramus superior of the stapedial a. leaves the tympanic cavity. The foramen faciale opens adjacent to the foramen for the ramus superior, as in the adult (see fig. VII-2).

1, ramus superior of stapedial a. passing through piriform fenestra; 2, stapedial a. (proximal portion); 3, chorda tympani; 4, tympanic n.; 5, insertion of stapedius m. on stapes.

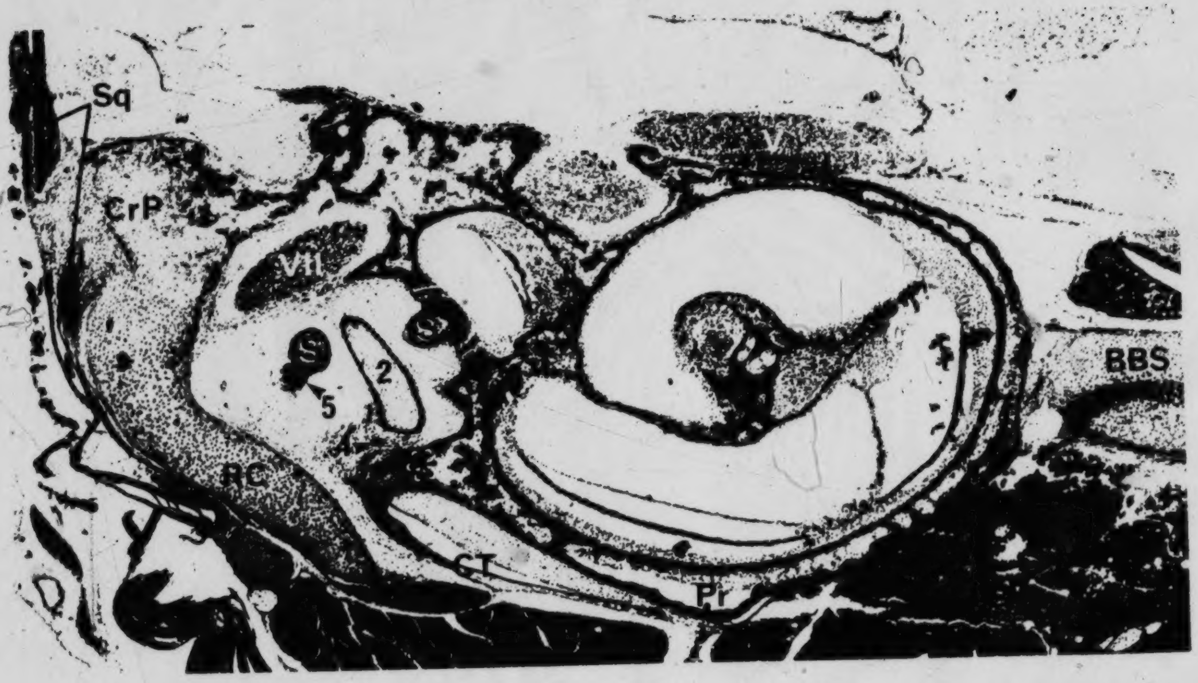

Sq
V
CrP
VII
S
S
2
5
BBS
RC
CT
Pt

FIG. VII-15 *H. semispinosus* MPIH 1964/45 (near-term fetus); s. 1524, cross-section, right side; Azan; x 37.

Proximal part of stapedial a. passing through obturator foramen of stapes. The asterisk indicates the start of the lateral section of the CTPP.

For key to numbered structures, see fig. VII-14.

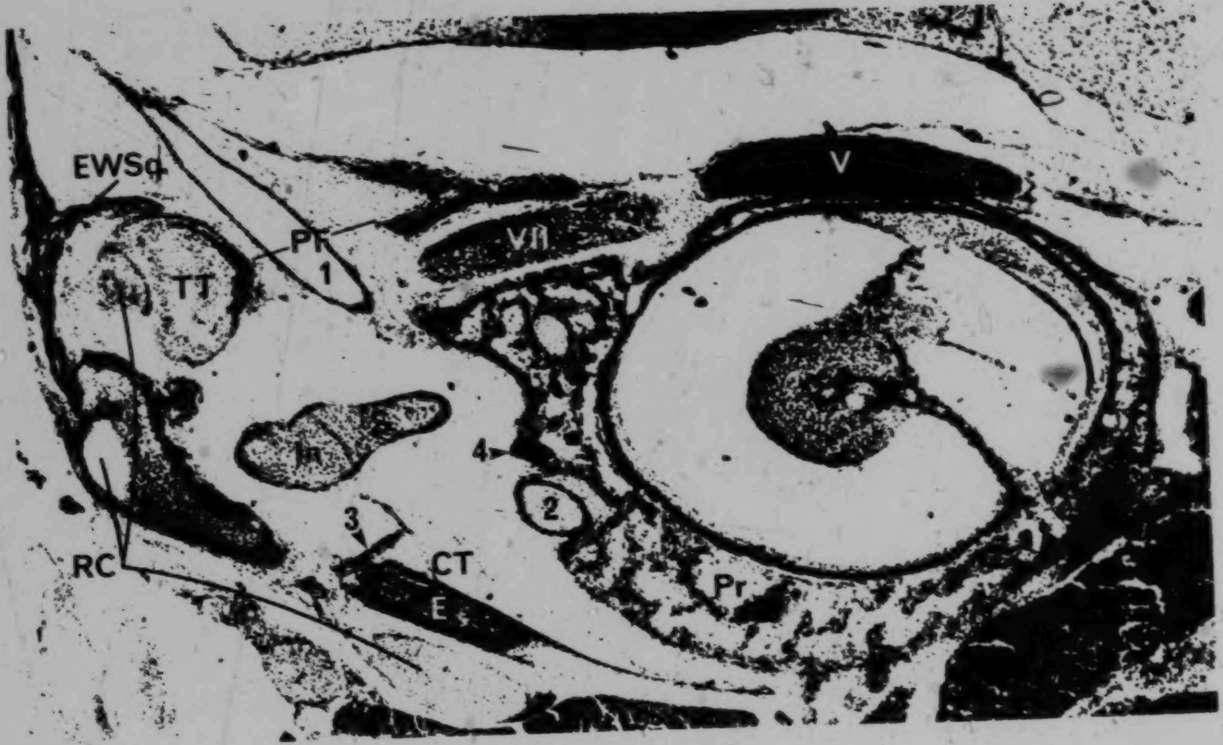

EWSd
Pr
1
TT
Su
V
VII
In
4
2
3
CT
E
RC
Pr

FIG. VII-16 *H. semispinosus* MPIH 1964/45 (near-term fetus); x. 1534, cross-section, right side; Azan; x 44.

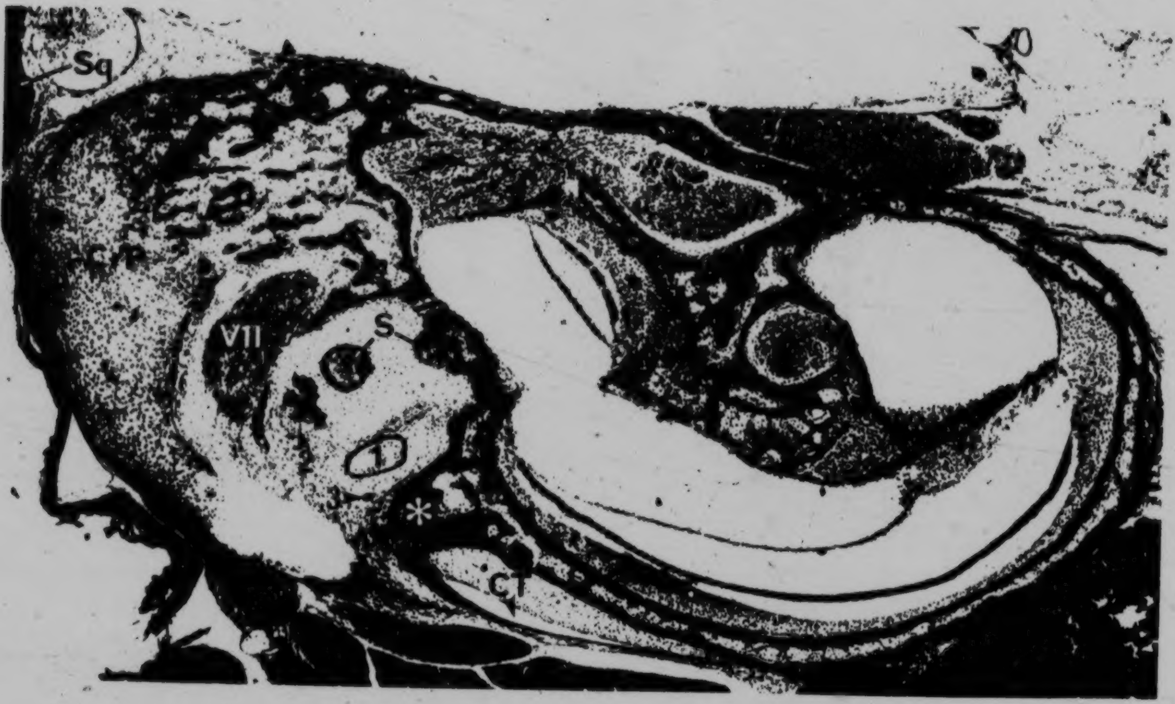
The proximal part of the stapedial a. has released the ramus posterior (1) beneath the stapes. The asterisk indicates the lateral section of the CTPP.

1, ramus posterior of the stapedial a.; 2, stapedius tendon; 3, tympanic n.

FIG. VII-17 *H. semispinosus* MPIH 1964/45 (near-term fetus); s. 1574, cross-section, right side (sides rev.); Azan; x 42.

The lateral section of the CTPP continues posteriorly along the underside of the auditory capsule (asterisk).

1, ramus posterior of the stapedial a.; 2, stapedius m.; 3, secondary tympanic membrane; 4, FMTC; 5, posterior continuation of crista parotica; 6, ramus auricularis vagi.


Sq
VII
S
I
*
CT

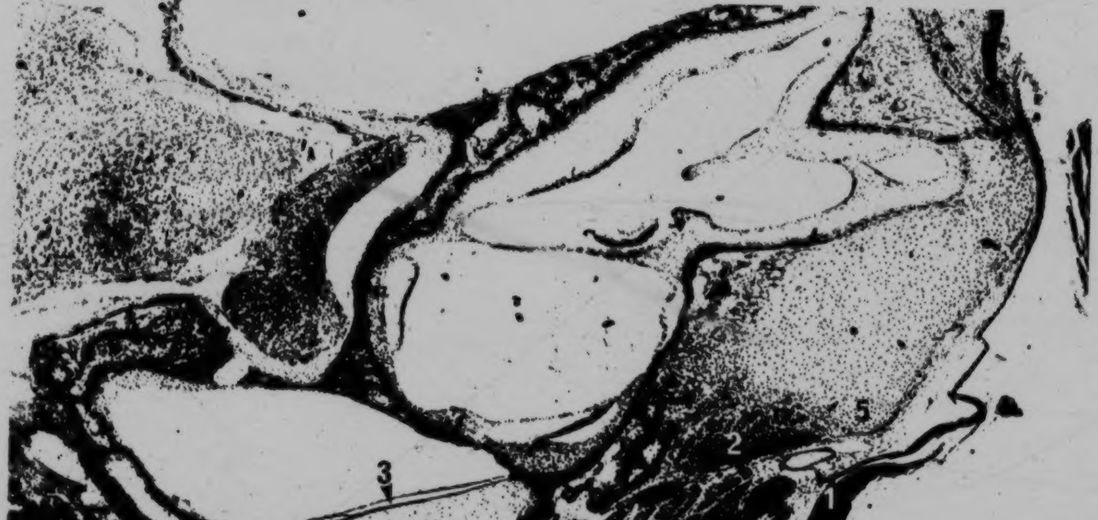

3
PTRA
4
CT
*
6
5
2
1

FIG. VII-18 _H_. _semispinosus_ MPIH 1964/45 (near-term fetus).

a. s. 1612, cross-section, right side (sides rev.); Azan; x 44.

b. s. 1630, cross-section, right side (sides rev.); Klüver-Barrera; x 44.

c. s. 1640, cross-section, right side (sides rev.); Klüver-Barrera; x 44.

The processus recessus posterior serves as the medial section of the CTPP, and meets the lateral section (asterisks) beneath the terminal part of D_3. The CTPP is quite insignificant in size even at this stage of development.

1, perilymphatic duct; 2, ramus posterior of the stapedial a.; 3, auricular ramus of the vagus travelling with tympanic n.

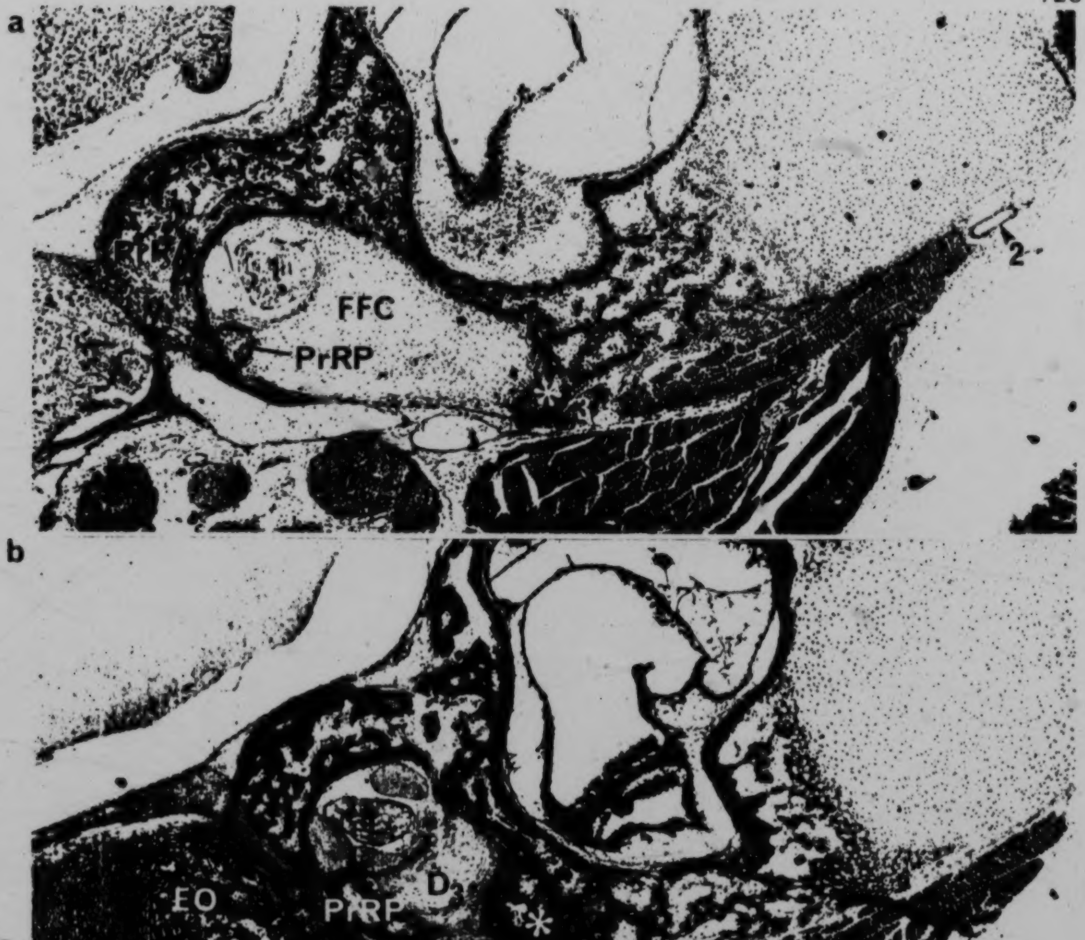

a
PrR
FFC
PrRP
*
2
b
EO
PrRP
D
*
c
1
EO

FIG. VII-19 S. setosus MPIH 1964/93 (fetus); s. 1660, cross-section, left side; Klüver-Barrera; x 30.

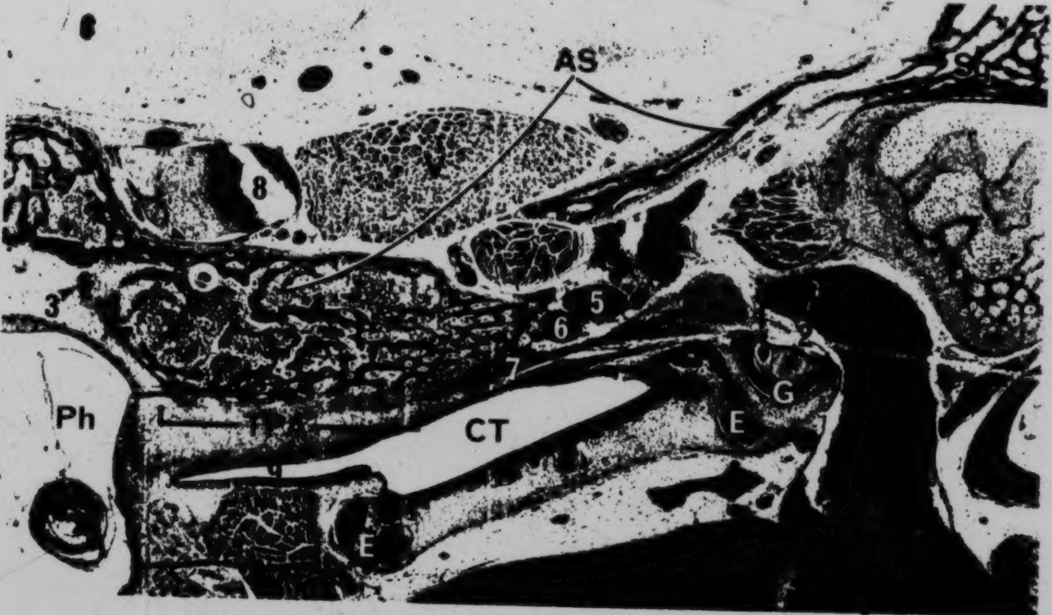
The posterior part of the pterygoid is very well-developed in S. setosus. Although it is fused to the sphenoid by this stage, bone derived from the pterygoid is probably represented in this section (3). This section passes through the area where the tympanic processes of the basisphenoid and alisphenoid adjoin (anteromedial angle of tympanic cavity). The cartilage of the tube is present above the lumen of the auditory tube, but it is in young cartilage and has taken up little stain.

1, chorda tympani; 2, Meckel's cartilage (degenerating); 3, ?pterygoid; 4, nerves of the pterygoid canal; 5, ramus inferior of the stapedial a; 6, vein; 7, lesser petrosal n.; 8, cavernous sinus; 9, lumen of auditory tube.

FIG. VII-20 S. setosus MPIH 1964/93 (fetus); s. 1680, cross-section, left side; Klüver-Barrera; x 30.

The tympanic processes of the basisphenoid and alisphenoid meet at the anteromedial angle of the presumptive tympanic cavity, and are thus difficult to separate in transverse sections of this region.

For key to numbered structures, see fig. VII-19.


AS
Sq
V
8
3
5
6
7
Ph
CT
G
E
E

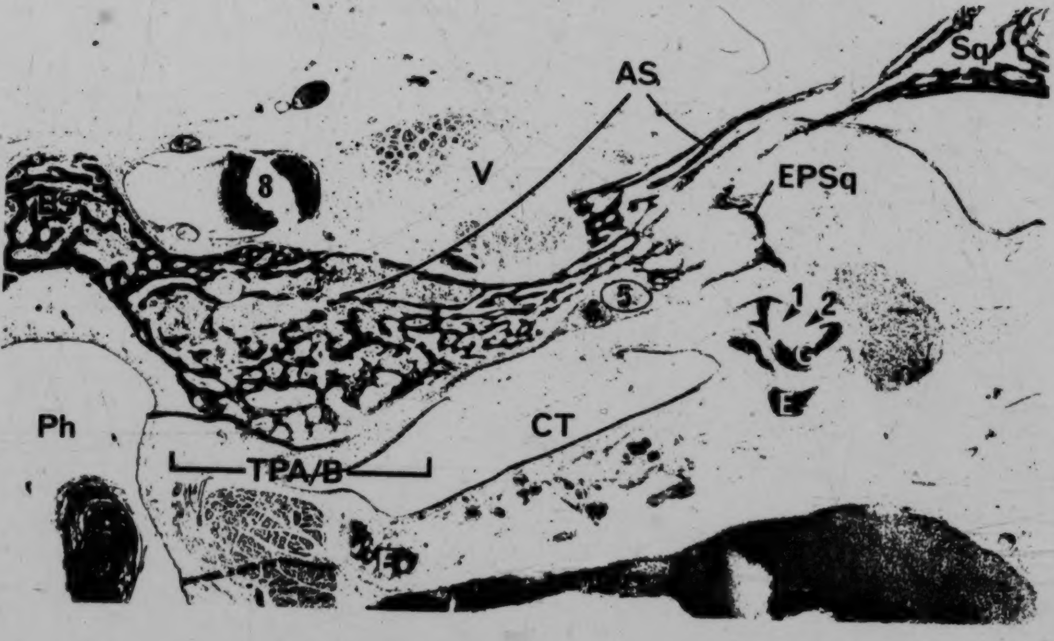

AS
Sq
EPSq
V
8
5
1
2
G
E
Ph
CT
TPA/B

FIG. VII-21 *S. setosus* MPIH 1964/93 (fetus); s. 1690, cross-section, left side; Klüver-Barrera; x 30.

As in the two preceding figures, the thickened portion of the alisphenoid represents the developing tympanic process of the alisphenoid. In the adult stage, the process completely surrounds the ramus inferior of the stapedial a. at its point of exit from the tympanic cavity.

For key to numbered structures, see fig. VII-22.

FIG. VII-22 *S. setosus* MPIH 1964/93 (fetus); x. 1770, cross-section, left side; Klüver-Barrera; x 30.

The posterior part of the piriform fenestra is largely closed over in this specimen, due to the development of the epitympanic wings of the petrosal and squamosal (cf. fig. VII-6).

1, chorda tympani; 2, ramus inferior of the stapedial a.; 3, internal carotid n.; 4, promontorial a.; 5, FMTC; 6, nerves of the pterygoid canal; 7, petrosquamous sinus in postglenoid foramen; 8, lesser petrosal n.; 9, greater petrosal n.; 10, tensor tympani m.

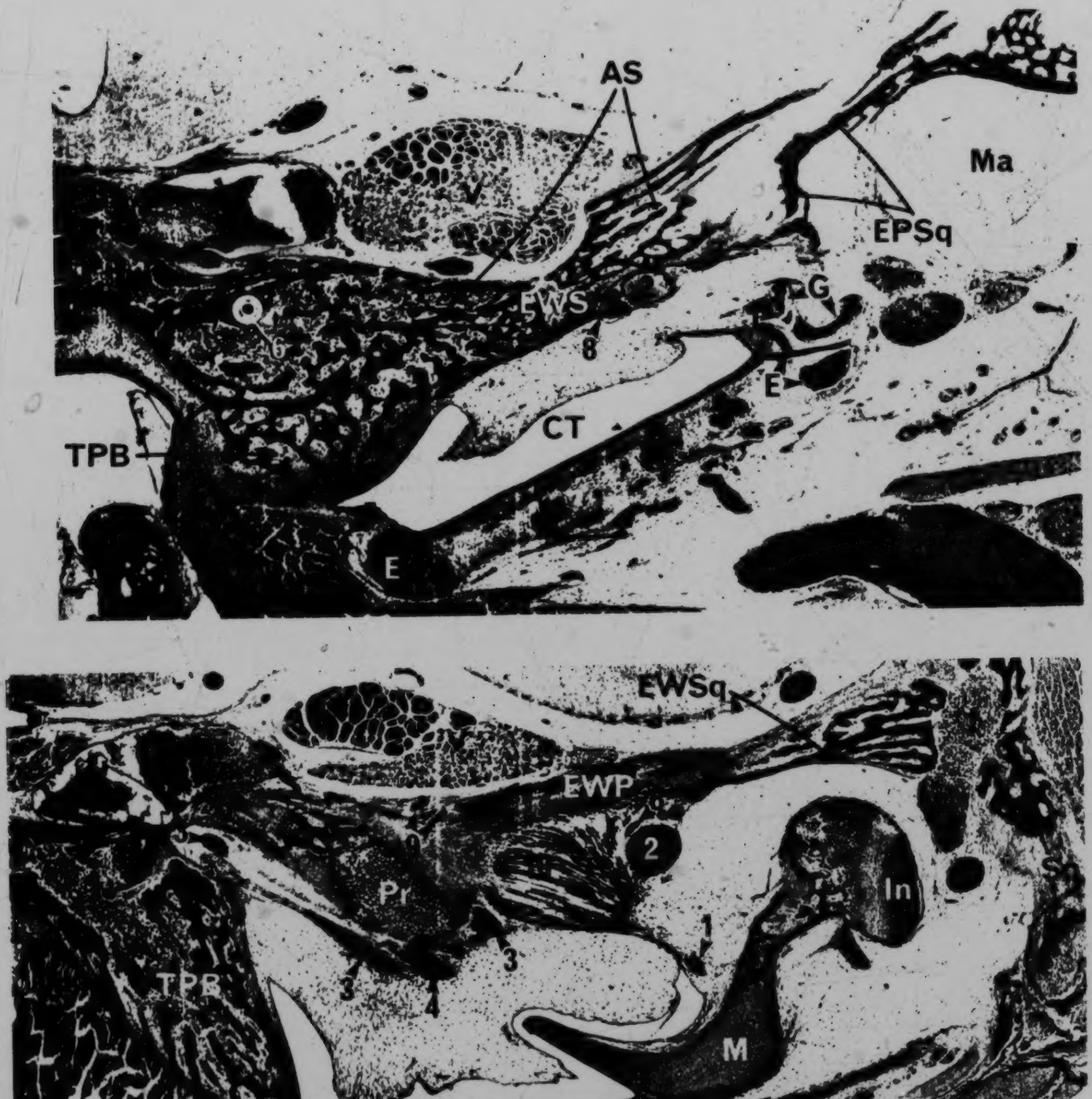

AS
Ma
EPSq
G
EWS
8
6
E
CT
TPB
E
EWSq
EWP
2
Pr
In
3
3
4
TPB
M
CT
E
5
RC

FIG. VII-23 S. setosus MPIH 1964/93 (fetus); x. 1800, cross-section, left side; Klüver-Barrera; x 30.

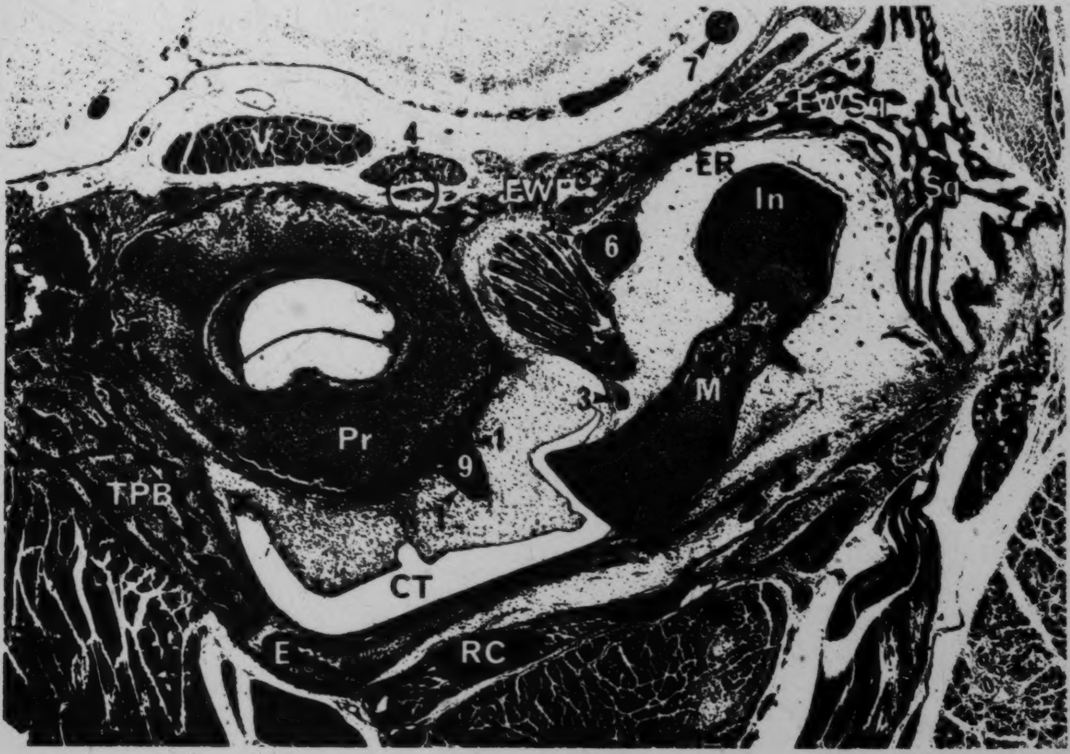
Section through middle of presumptive tympanic cavity.

1, internal carotid n.; 2, geniculate ganglion; 3, chorda tympani; 4, greater petrosal n. arising from geniculate ganglion; 5, tympanic plexus and tympanic n.; 6, ramus inferior of the stapedial a.; 7, ramus superior of the stapedial a.; 8, ?element of Spence; 9, promontorial a.; 10, proximal stapedial a. dividing into ramus superior and ramus inferior.

FIG. VII-24 S. setosus MPIH 1964/93 (fetus); s. 1830, cross-section, left side; Klüver-Barrera; x 30.

Section through middle of presumptive tympanic cavity.

For key to numbered structures, see fig. VII-23.


7
EWSq
V
4
EWP
ER
In
Sq
6
3
M
Pr
1
9
TPB
1
CT
E
RC

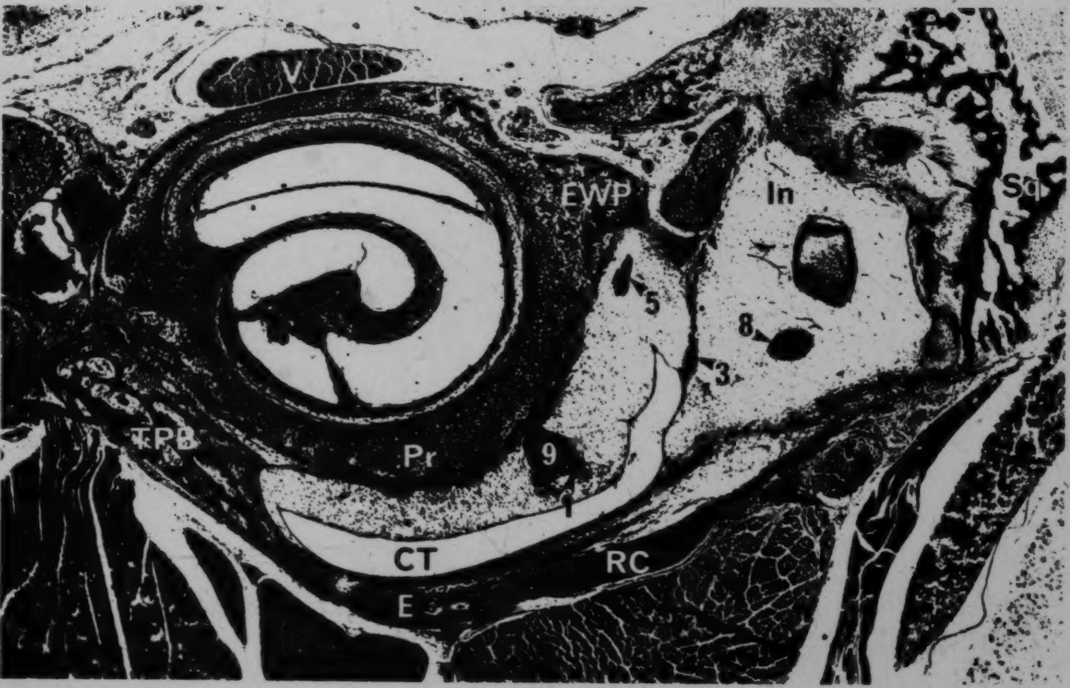

V
EWP
In
Sq
5
8
3
TPB
Pr
9
1
CT
RC
E

FIG. VII-25 S. setosus MPIH 1964/93 (fetus).

- a. s. 1970, cross-section, right side (sides rev.); Klüver-Barrera; x 30.
- b. s. 1980, cross-section, right side (sides rev.); Klüver-Barrera; x 30.
- c. s. 1990, cross-section, right side (sides rev.); Klüver-Barrera; x 30.

The processus recessus posterior (6) is in young cartilage and is not distinctly stained. The medial section of the CTPP eventually develops from this processus (cf. fig. VII-18). The lateral section of the CTPP (asterisks) is more distinct, but it is small.

1, posterior continuation of crista parotica; 2, secondary tympanic membrane; 3, ramus posterior of the stapedial a.; 4, ramus auricularis vagi; 5, FMTC; 6, processus recessus posterior; 7, stapedius m.

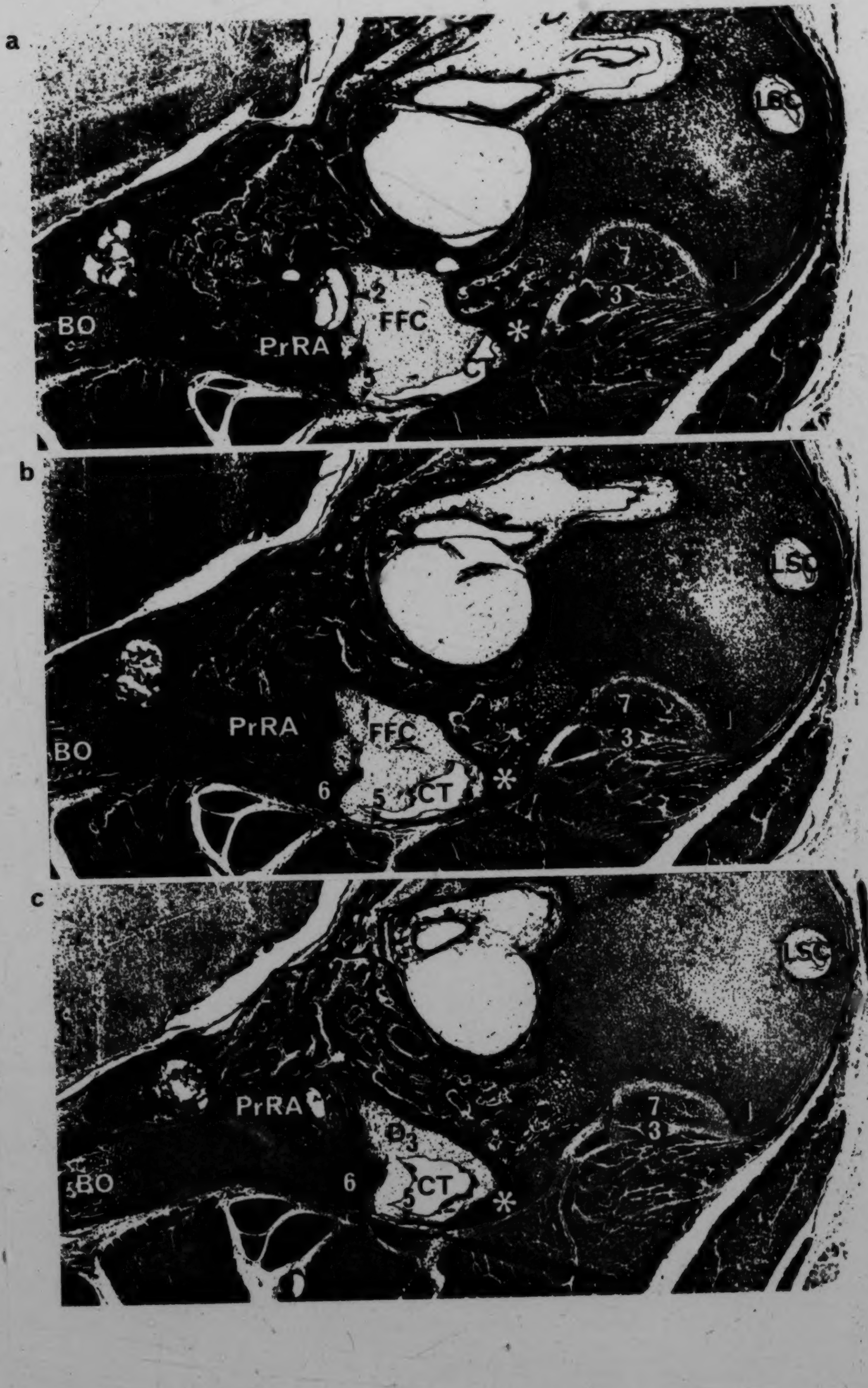

a
LSC
7
3
2
FFC
BO
PrRA
*
C
5
b
LSC
PrRA
FFC
BO
7
3
*
6
5
CT
c
LSC
PrRA
D
3
7
3
BO
6
CT
5
*

FIG. VII-26 *M. dobsoni* MPIH 1964/103 (fetus); s. 990, cross-section, left side; Gabe; x 63.

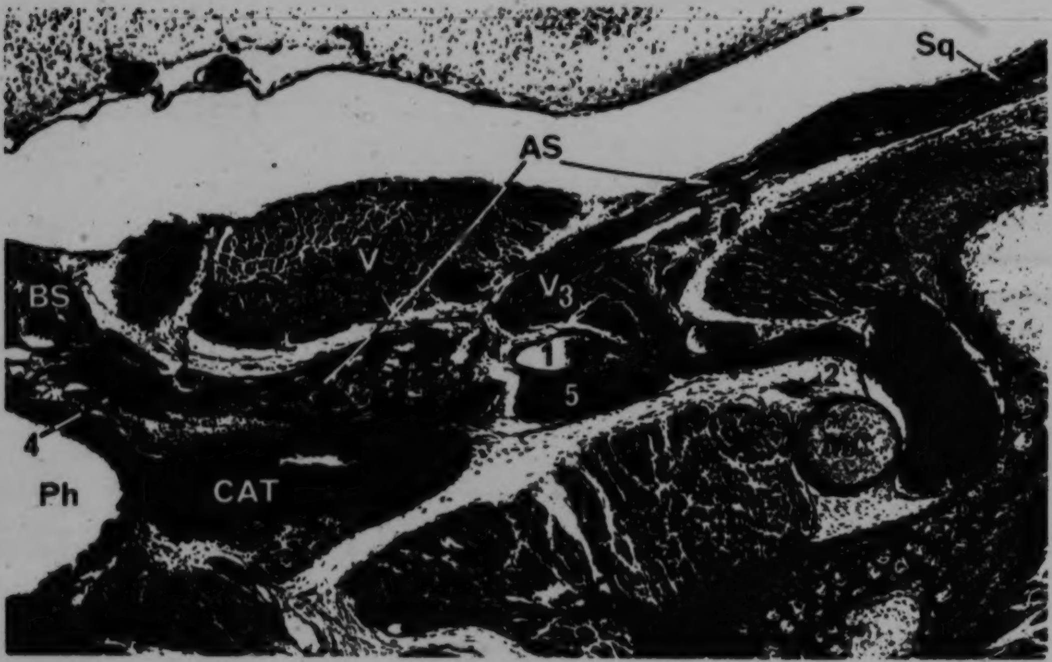
The posterior part of the pterygoid bone (4) has not yet fused to the undersurface of the basisphenoid. Note that its site of termination is directly above the cartilage of the tube (cf. fig. VII-27).

1, ramus inferior of the stapedial a.; 2, chorda tympani; 3, nerves of the pterygoid canal; 4, pterygoid bone; 5, otic ganglion; 6, lesser petrosal n.

FIG. VII-27 *M. dobsoni* MPIH 1964/103 (fetus); s. 1010, cross-section, left side; Gabe; x 63.

Section through anterior end of cavum tympani.

For key to numbered structures, see fig. VII-26.


Sq
AS
V
V3
BS
1
5
2
4
Ph
CAT

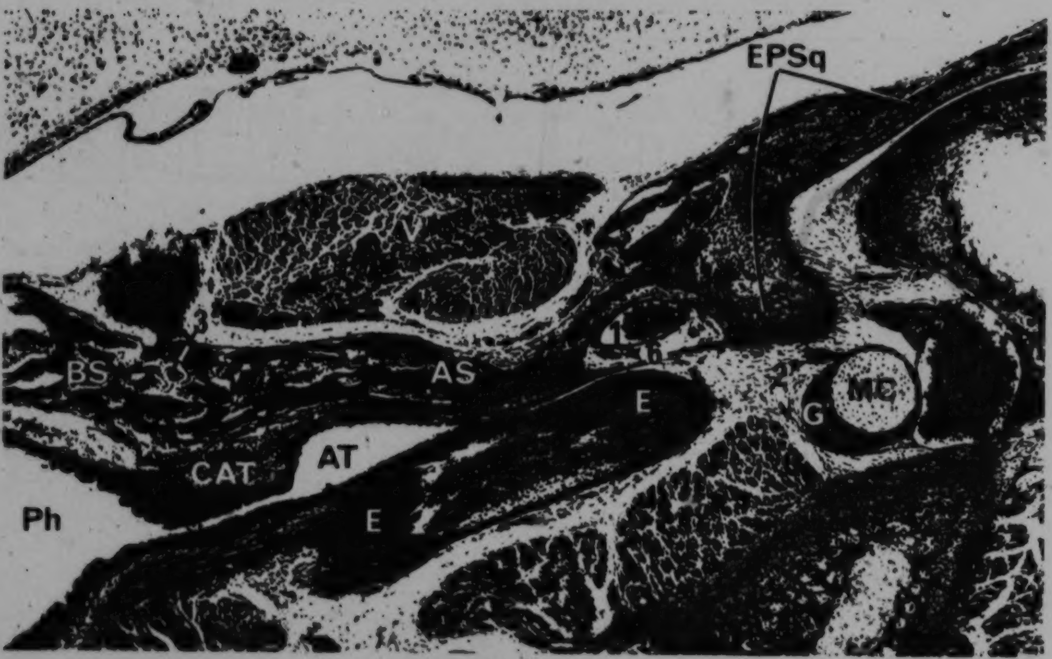

EPSq
V
3
BS
AS
1
6
2
MC
G
E
CAT
AT
Ph
E

FIG. VII-28 M. dobsoni MPIH 1964/103 (fetus); s. 1094, cross-section, left side; Klüver-Barrera; x 47.

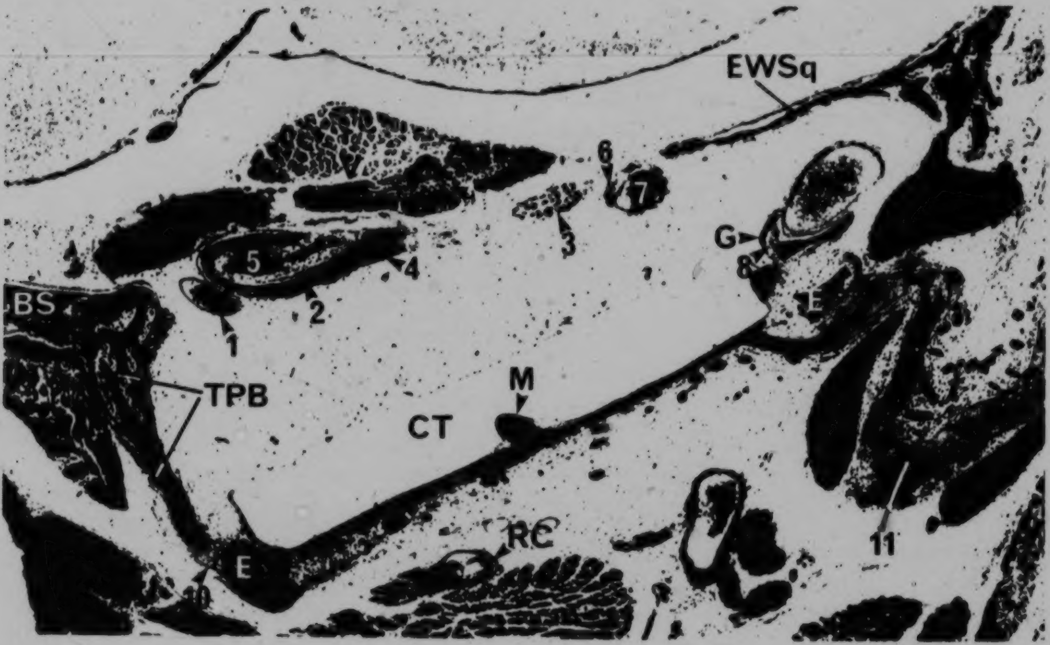
Section through anterior carotid foramen. A process of the basisphenoid has encircled the degenerating alicochlear commissure (2).

1, promontorial a.; 2, process of basisphenoid surrounding alicochlear commissure; 3, tensor tympani; 4, deep petrosal and greater petrosal nn.; 5, alicochlear commissure; 6, lesser petrosal n.; 7, ramus inferior of the stapedial a.; 8, chorda tympani; 9, ramus superior of the stapedial a.; 10, FMTC; 11, external acoustic meatus.

FIG. VII-29 M. dobsoni MPIH 1964/103 (fetus); s. 1164, cross-section, left side; Klüver-Barrera; x 41.

Section through anterior end of tegmen tympani. In the adult, the foramen faciale is separate from the foramen for the ramus superior (cf. figs. VII-1, VII-14).

For key to numbered structures, see fig. VII-28.


EWSq
V
6
7
3
G
8
E
5
4
2
1
BS
TPB
M
CT
RC
E
10
11

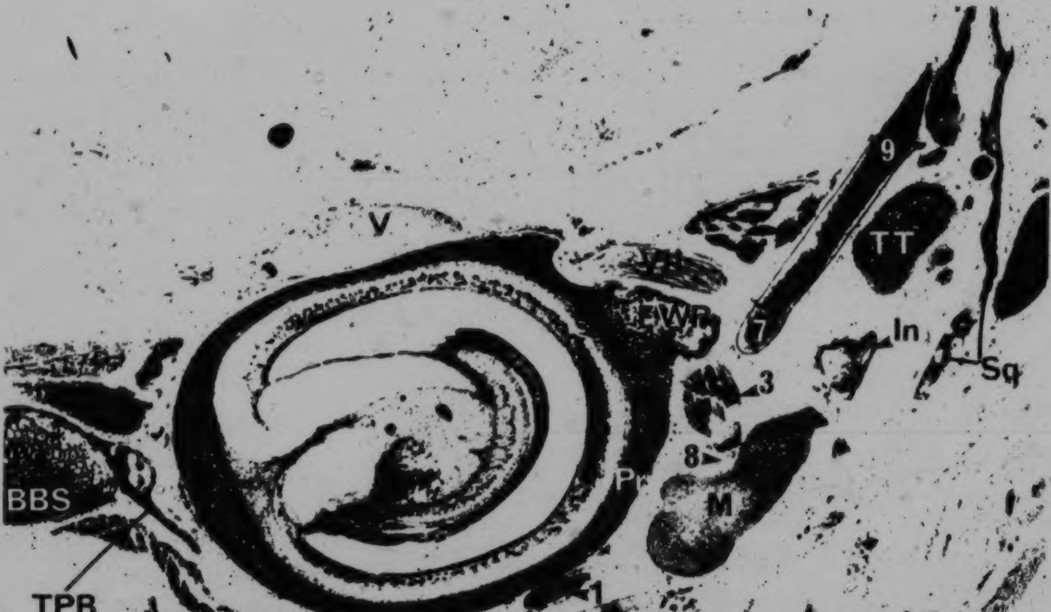

9
V
V
TT
EWP
7
In
3
Sq
8
P
M
BBS
TPB
1
RC
10
E

FIG. VII-30 *M. dobsoni* MPIH 1964/103 (fetus).

a. s. 1254, cross-section, left side; Klüver-Barrera; x 56.

b. s. 1264, cross-section, left side; Klüver-Barrera; x 56.

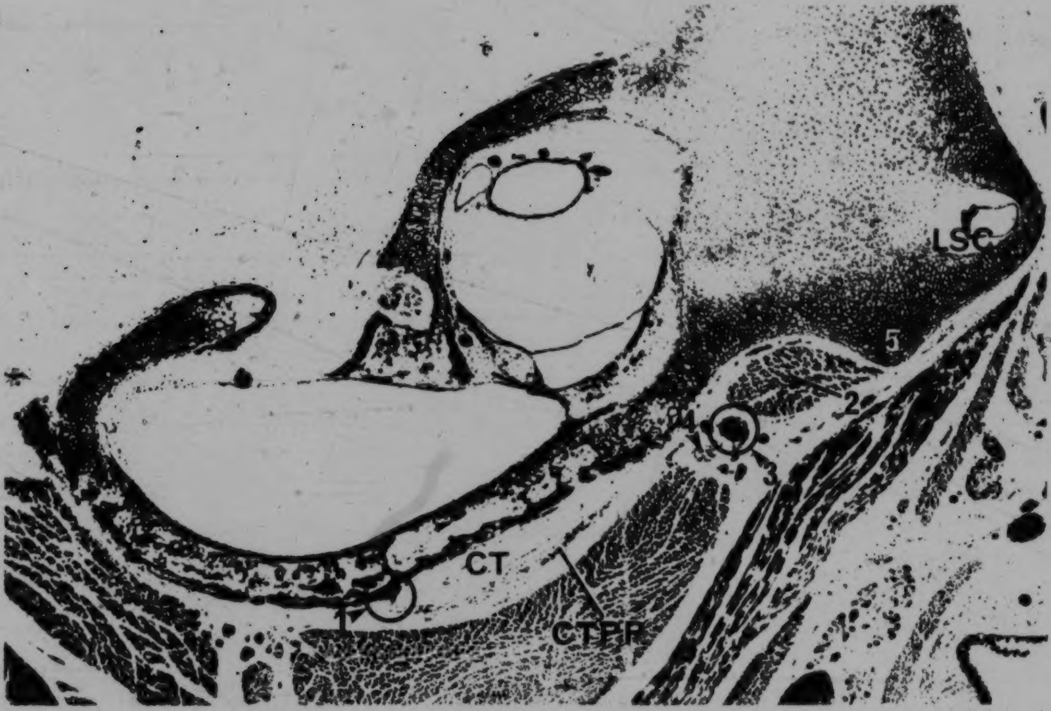
c. s. 1264, cross-section, right side (sides rev.); Klüver-Barrera; x 56.

d. s. 1274, cross-section, right side (sides rev.); Klüver-Barrera; x 56.

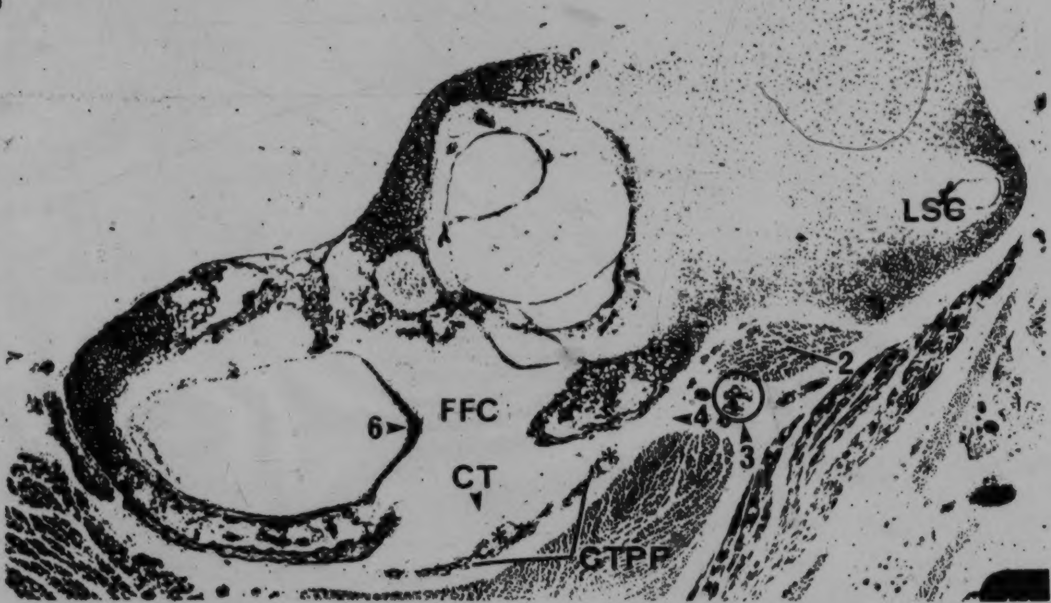
Series of sections through the caudal tympanic process of the petrosal. The caudal tympanic process of Oryzorictinae is relatively larger than in Tenrecinae (see fig. VII-3) and completely covers the apertura fossulae fenestrae cochleae. Cartilage 'islands' may still be seen in the anterior rim of the process (asterisks). The small eminence on the ventral surface of the promontory (1) may represent a tiny rostral tympanic process of the petrosal.

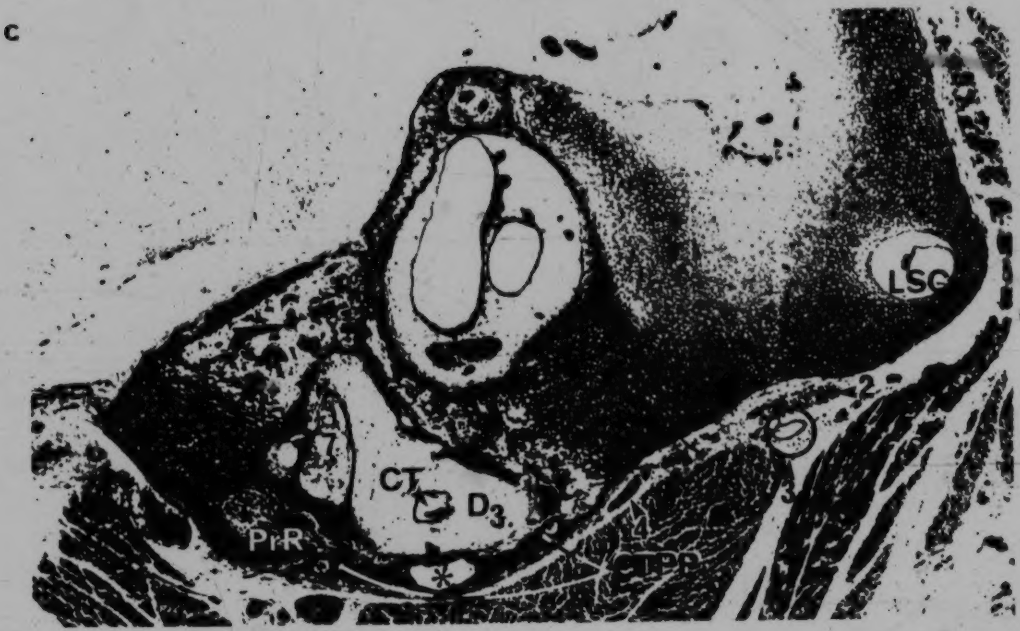
1, ?rostral tympanic process of the petrosal; 2, stapedius m.; 3, ramus posterior of the stapedial a.; 4, ramus auricularis of the vagus n. (?with tympanic n.); 5, posterior continuation of crista parotica; 6, secondary tympanic membrane; 7, perilymphatic duct.

a


LSC
5
2
4
3
1
CT
CTPP

b


LSC
2
FFC
6
4
3
CT
CTPP


c
LSC
2
3
7
CT
D3
PrR
*
C1PP

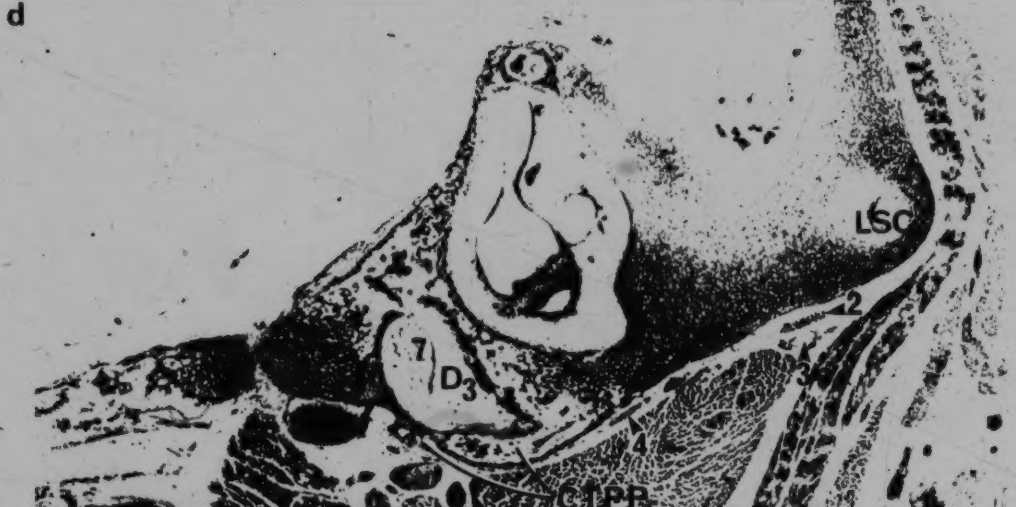

d
LSC
2
3
7
D3
4
C1PP

FIG. VII-31 Solenodon sp. MPIH 6863 (juvenile); s. 1119, cross-section, right side; Azan; x 25.

Section through auditory tube, in advance of cavum tympani. The only outgrowth on the basisphenoid which conforms to McDOWELL's tympanic process of the basisphenoid is the small ridge (6) adjacent to the tubal cartilage (cf. fig. VII-4). However, the relationship of this ridge to the pterygoid canal (5) suggests that the ridge may be pterygoidal rather than basisphenoidal in origin.

1, chorda tympani in groove on the entoglenoid process of the squamosal; 2, ramus inferior of the stapedial a.; 3, lesser petrosal n.; 4, lateral part of tympanic process of the alisphenoid; 5, nerves of the pterygoid canal; 6, ?tympanic process of basisphenoid.

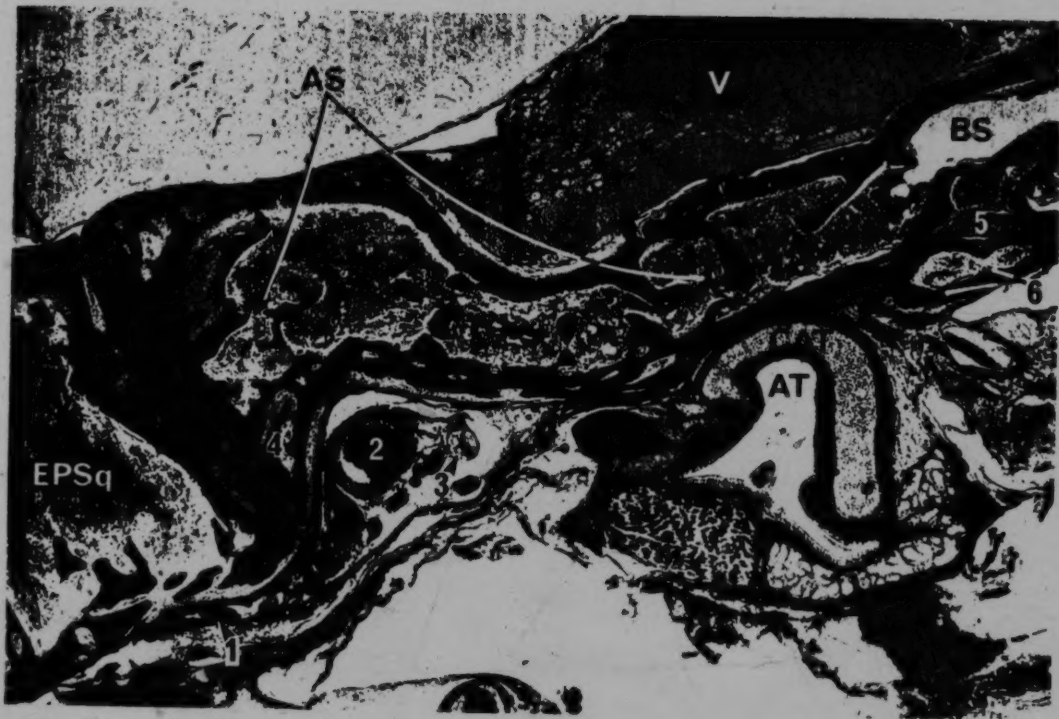

AS
V
BS
5
6
AT
4
2
3
EPSq
1

FIG. VII-32 Solenodon sp. MPIH 6863 (juvenile); s. 1318, cross-section, right side, Azan; x 16.

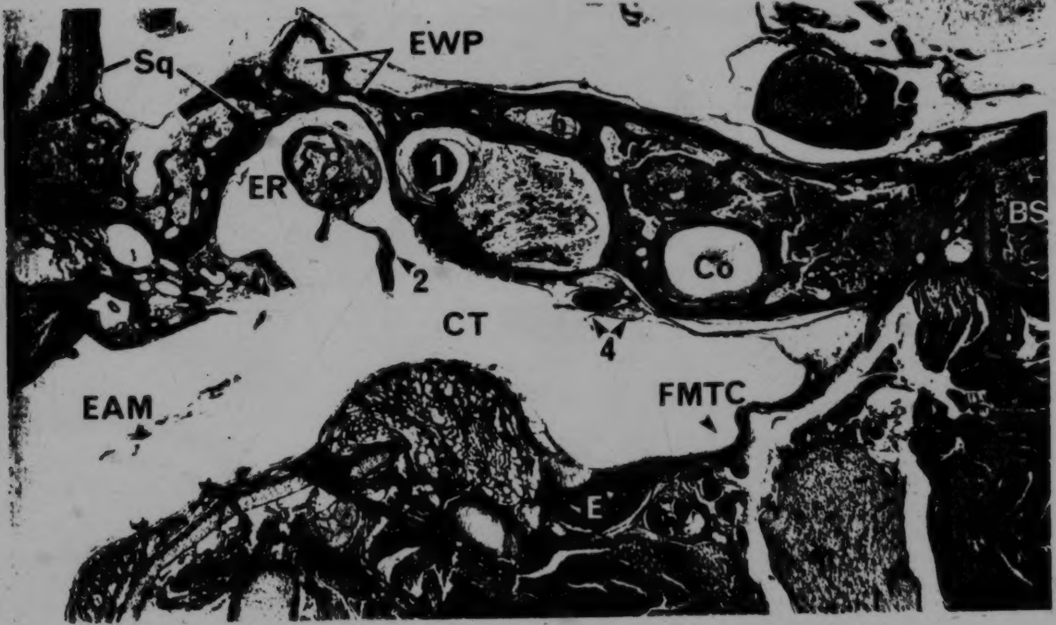
Section through anterior pole of promontory. Note thick fibrous membrane of the tympanic cavity.

1, ramus inferior of the stapedial a.; 2, chorda tympani; 3, tensor tympani; 4, internal carotid n. and promontorial a.; 5, tympanic n.; 6, geniculate ganglion; 7, auricular cartilage.

FIG. VII-33 Solenodon sp. MPIH 6863 (juvenile); s. 1354, cross-section, right side; Azan; x 25.

Section through middle of promontory.

For key to numbered structures, see fig. VII-32.


Sq
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2
Co
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CT
4
EAM
FMTC
E

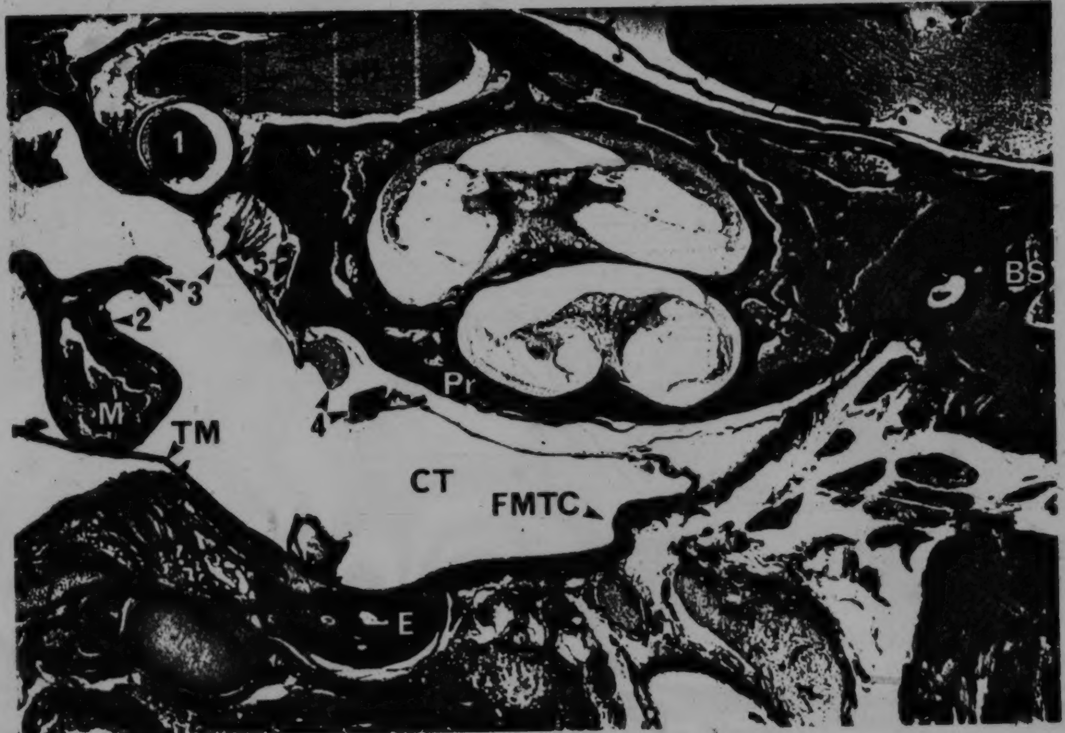

1
BS
3
5
2
M
TM
4
Pr
CT
FMTC
E

FIG. VII-34 Solenodon sp. MPIH 6863 (juvenile); s. 1418, cross-section, right side; Azan.

a. Section through posterior carotid foramen; x 16.

b. Enlargement of area of articulation between the posterior crus of the ectotympanic and the caudal tympanic process of the petrosal. Secondary cartilage can be detected at the place of articulation, indicating that the two bone territories are in the process of fusion (arrows); x 47.

1, tendon of stapedius m.; 2, internal carotid a.; 3, tympanic n.; 4, internal carotid n.; 5, ramus posterior of the stapedial a. (branch to pinna); 6, tympano-styloid cartilage; 7, FMTC; 8, cranial cervical ganglion.

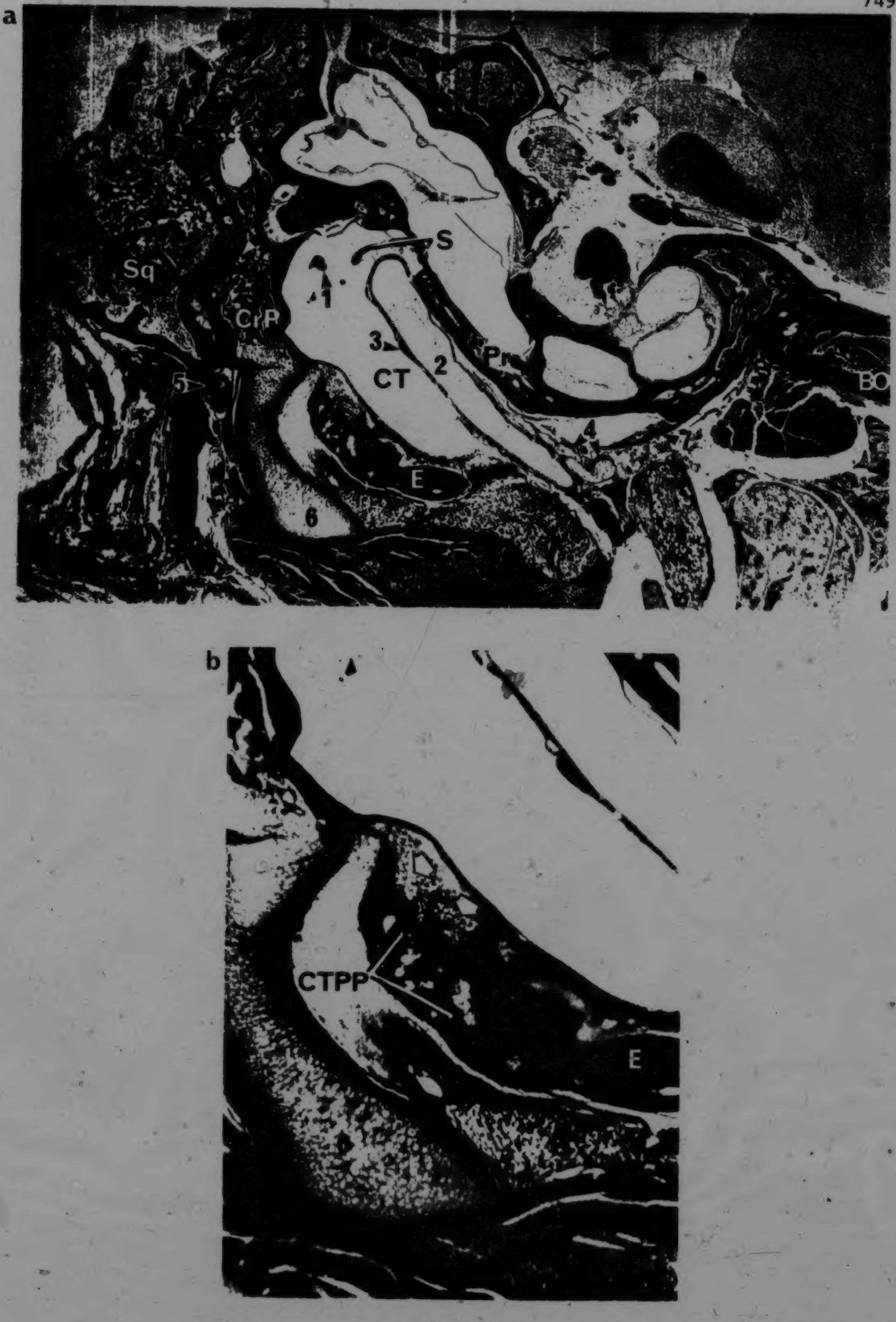

a
S
Sq
1
CrP
3
CT
2
Pr
5
BO
4
E
6
b
CTPP
E

FIG. VII-35 Solenodon sp. MPIH 6863 (juvenile); s. 1431, cross-section, left side; Azan; x 16.

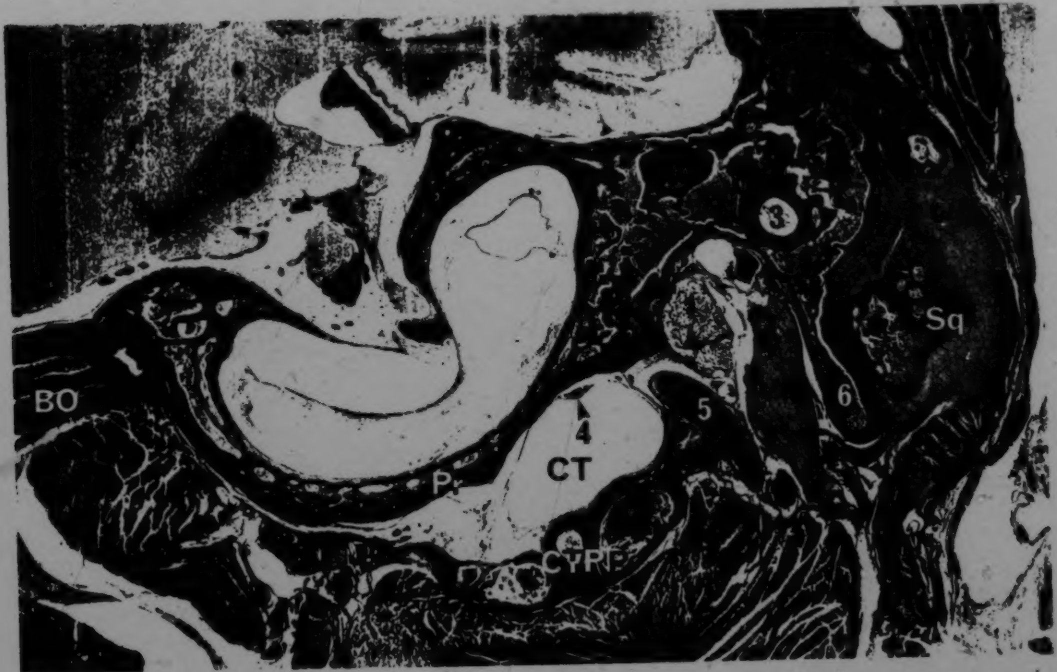
Section through anterior end of caudal tympanic process of the petrosal. The ramus posterior of the stapedial a. cuts across this process as it leaves the tympanic cavity.

1, stapedius m.; 2, secondary tympanic membrane; 3, lateral semicircular canal; 4, tympanic n.; 5, ramus posterior of stapedial a.; 6, posterior continuation of crista parotica; 7, auricular ramus of the vagus.

FIG. VII-36 Solenodon sp. MPIH 6863 (juvenile); s. 1462, cross-section, left side; Azan; x 16.

As the ramus posterior leaves the tympanic cavity, it divides into branches. One or two small twigs continue posteriorly beneath the stapedius m. (this figure); another, large branch travels anteriorly towards the pinna (fig. VII-34a).

For key to numbered structures, see fig. VII-35.


3
Sq
6
BO
4
5
CT
P
D
CYRP

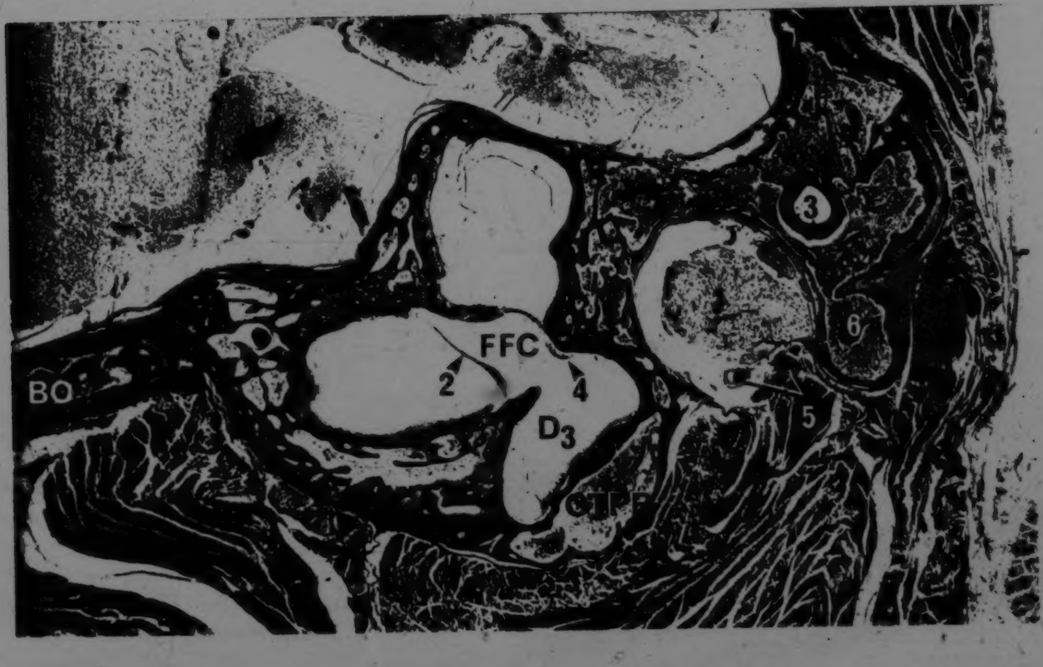

3
6
FFC
BO
2
4
5
D$_3$
CTPP

FIG. VIII-1 Relationships of the ectotympanic to other components of the ventral wall.

This figure schematically illustrates how the phaneric, semiphaneric, and aphaneric conditions of the ectotympanic are controlled by the presence or relative intensity of three ontogenetic factors (growth, pneumatization, and soft-tissue influences). For explanation, see text (section 8.1.5.3).

1 - sutural tissues form

1^1 - sutural tissues do not form, or form incompletely

2 - tympanic process grows significantly

2^1 - tympanic process does not grow significantly

3 - degree of pneumatization is significant

3^1 - degree of pneumatization is insignificant

Co, cochlea; Ec, ectotympanic; FM, fibrous membrane; TP, tympanic process.

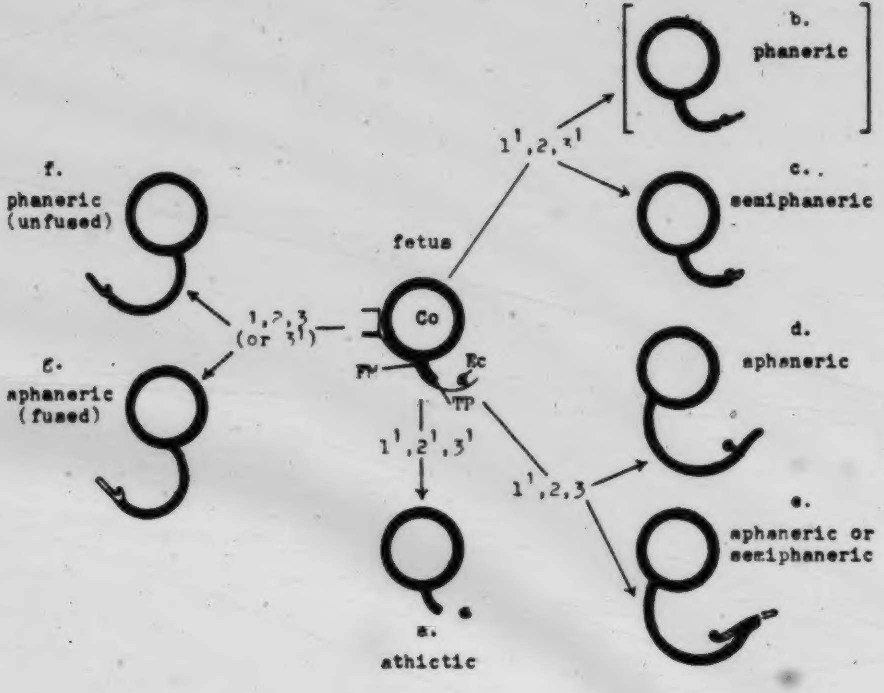

f.
phaneric
(unfused)
g.
aphaneric
(fused)
1,2,3
(or 3')
fetus
Co
FM
Ec
TP
1',2',3'
a.
athictic
1',2,3'
b.
phaneric
c.
semiphaneric
1',2,3
d.
aphaneric
e.
aphaneric or
semiphaneric

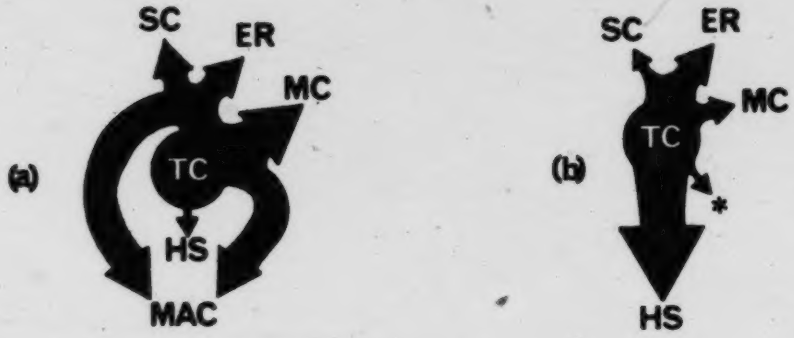
FIG. VIII-2 Schematic depiction of the progress of middle ear pneumatization in lorises (a) and lemurs (b).

The central circle (TC) represents the limits of the tympanic cavity proper immediately before the onset of pneumatization. The arrows indicate, in a rough way, the major trajectories of pneumatic activity and the relative positions of principal spaces in the adult stage.

The lorisiform pattern is characterized by intense pneumatic activity in the central and posterior parts of the dorsal wall. There is almost no pneumatization in the ventral part of the tympanic cavity, and hence the hypotympanic sinus is barely indicated in the adult (indicated by the narrow width of its arrow).

The lemuriform pattern is effectively the reverse. The ventral wall is strongly affected by pneumatization; the central and posterior parts of the dorsal wall are pneumatized to some extent, but never to the degree seen in lorises.

ER, epitympanic recess; HS, hypotympanic sinus; MAC, medial accessory cavity; MC, mastoid cavity; SC, supracochlear cavity; *, innominate diverticulum associated with the posterior septum.


(a)
SC
ER
MC
TC
HS
MAC
(b)
SC
ER
MC
TC
*
HS

BIBLIOGRAPHY

Abbreviations conform to entries in *Biosis* list of serials (BioSciences Information Service of Biological Abstracts, Philadelphia 1975). Style of citation is that employed by the journal *Folia primatologica* (Karger, Basel).

ADAMS, W.E.: The extracranial carotid rete and carotid fork in *Nycticebus coucang*. Ann. Zool., Agra *2*:21-37 (1957).

ALLEN, J.A.: The external ear bone in certain rodents. Bull. am. Mus. nat. Hist. *20*:135-138 (1904).

ALLEN, J.A.: Notes on *Solenodon paradoxus* Brandt. Bull. am. Mus. nat. Hist. *24*:505-517 (1908).

ANSON, B.J.; BAST, T.H., and RICHANY, S.F.: The fetal and early post-natal development of the tympanic ring and related structures in man. Ann. Otol. Rhinol. Laryngol. *57*:103-128 (1955).

ANSON, B.J. and DONALDSON, J.A.: The surgical anatomy of the temporal bone and ear; 2nd ed. (Saunders, Philadelphia 1973).

AREY, L.B.: Developmental anatomy, a textbook and laboratory manual of embryology; rev. 7th ed. (Saunders, Philadelphia 1974).

ASK-UPMARK, E.: On the entrance of the carotid cartery into the cranial cavity in *Stenops gracilis* and *Otolicnus crassicaudatus*. Acta anat. *19*:101-103 (1953).

BÄHLER, H.: Das Primordialcranium des Halbaffen *Microcebus murinus*; med. Diss. Bern (1938).

BAKER, M.A.: Influence of the carotid rete on brain temperature in cats exposed to hot environments. J. Physiol., Lond. *220*:711-728 (1972).

BAKER, M.A. and HAYWARD, J.N.: Carotid rete and brain temperature of cat. Nature, Lond. *216*:139-141 (1967).

BAKER, M.A. and HAYWARD, J.N.: The influence of the nasal mucosa and the carotid rete upon hypothalamic temperature in sheep. J. Physiol., Lond. *198*:561-579 (1968).

BAST, T.H. and ANSON, B.J.: The temporal bone and the ear (Charles C. Thomas, Springfield 1949).

BAST, T.H. and FORESTER, H.B.: Origin and distribution of air cells in the temporal bone. Arch. Otolaryngol. *30*:225-249 (1939).

BATSON, O.V.: The applied anatomy of the temporal bone; in G.M. ENGLISH Otolaryngology, vol. 1, ch. 2, pp. 1-20 (Harper & Row, Hagerstown 1976).

BAXTER, J.S.: Frazer's manual of embryology; 3rd ed. (Baillière, Tindall and Cox, London 1953).

BEER, G.R. DE: Studies on the vertebrate head. II. The orbitotemporal region of the skull. Q.J. microsc. Sci. 70:263-370 (1926).

BEER, G.R. DE: The development of the skull of the shrew. Phil Trans. R. Soc. Lond. B217:411-480 (1929).

BEER, G.R. DE: The development of the vertebrate skull (Clarendon Press, Oxford 1937).

BEER, G.R. DE: Embryos and ancestors; 3rd ed. (Clarendon Press, Oxford 1958).

BEER, G.R. DE and WOODGER, J.H.: The early development of the skull in the rabbit. Phil. Trans. R. Soc. Lond. B218:373-414 (1930).

BLOOM, W. and FAWCETT, D.W.: A textbook of histology; 9th ed. (Saunders, Philadelphia 1968).

BONDY, G.: Beiträge zur vergleichenden Anatomie des Gehörorgans der Säuger (Tympanicum, Membrana Shrapnelli und Chordaverlauf). Anat. Hefte 34:293-408 (1907).

BOULAY, G.H. DU and VERITY, P.M.: The cranial arteries of mammals (Heinemann, London 1973).

BROERS, C.-J.: La position taxonomique de Tupaia parmi les primates basée entre autres sur la structure de sa caisse du tympan (communication préliminaire). C.R. Assoc. Anat. 116:361-375 (1963).

BROMANN, I.: Die Entwickelungsgeschichte der Gehörknöchelchen beim Menschen. Anat. Hefte 11:507-670 (1899).

BROOM, R.: On the structure of the skull in Chrysochloris. Proc. zool. Soc. Lond. 1916:449-459 (1916).

BROTERENBROOD, E.C.: Concise catalogue of the central embryological collection of the Hubrecht laboratory (Hubrecht Laboratory, Utrecht 1977).

BUGGE, J.: The cephalic arterial system in the insectivores and primates with special reference to the Macroscelidoidea and Tupaioidea and the insectivore-primate boundary. Z. Anat. Entwicklungsgesch. 135:274-300 (1972).

BUGGE, J.: The cephalic arterial system in insectivores, primates, rodents, and lagomorphs, with special reference to the systematic classification. Acta anat. 87:suppl 62, pp. 1-160 (1974).

BUTLER, P.M.: On the evolution of the skull and teeth in the Erinaceidae, with special reference to fossil material in the British Museum. Proc. zool. Soc. Lond. 1948:446-500 (1948).

BUTLER, P.M.: The skull of *Ictops* and the classification of the Insectivora. Proc. zool. Soc. Lond. 1956:453-481 (1956).

BUTLER, P.M.: Insectivores and bats from the Miocene of East Africa: new material; in L.S.B. LEAKEY Fossil vertebrates of Africa, vol. 1, pp. 1-37 (Academic Press, London 1969).

BUTLER, P.M.: The problem of insectivore classification; in K.A. JOYSEY and T.R. KEMP Studies in vertebrate evolution, pp. 253-265 (Oliver and Boyd, Edinburgh 1972).

BUTLER, P.M. and HOPWOOD, A.T.: Insectivora and Chiroptera from the Miocene rocks of Kenya Colony. Br. Mus. nat. Hist. foss. Mamm. Afr. 13:1-35 (1957).

CAMPBELL, C.B.G.: Taxonomic status of tree shrews. Science, N.Y. 153:436 (1966).

CARLSSON, A.: Die Macroscelididae und ihre Beziehungen zu den übrigen Insectivoren. Zool. Jahrb., Abt. Syst., Ökol., Geogr. 28:349-400 (1909).

CARTMILL, M.: Arboreal adaptations and the origin of the order primates; in R. TUTTLE The functional and evolutionary biology of primates, pp. 97-122 (Aldine, Chicago 1972).

CARTMILL, M.: Rethinking primate origins. Science, N.Y. 184:436-443 (1974).

CARTMILL, M.: Strepsirhine basicranial structures and the affinities of the Cheinogaleidae; in W.P. LUCKETT and F.S. SZALAY Phylogeny of the primates, a multidisciplinary approach, pp. 313-354 (Plenum Press, N.Y. 1975).

CHARLES-DOMINIQUE, P. and MARTIN, R.D.: Evolution of lorises and lemurs. Nature, Lond. 227:257-260 (1970).

CLARK, W.E. LE GROS: On the skull of *Tupaia*. Proc. zool. Soc. Lond. 1925:559-567 (1925).

CLARK, W.E. LE GROS: On the anatomy of the pentailed tree shrew (*Ptilocercus lowii*). Proc. zool. Soc. Lond. 1926:1179-1309 (1926).

CLARK, W.E. LE GROS: The brain of Insectivora. Proc. zool. Soc. Lond. 1933:975-1013 (1933).

CLARK, W.E. LE GROS: Early forerunners of man (Baillière, Tindall and Cox, London 1934).

CLARK, W.E. LE GROS: The antecedents of man, an introduction to the evolution of the primates; 1st ed. (Edinburgh University Press, Edinburgh 1959).

CLARK, W.E. LE GROS: The antecedents of man, an introduction to the evolution of the primates; 3rd ed. (Quadrangle Books, Chicago 1971).

CLEMENS, W.: Fossil mammals of the type Lance Formation, Wyoming. Part 2, Marsupialia. Univ. Calif. Publ. Geol. Sci. 62:1-122 (1966).

CLEMENS, W.: *Purgatorius*, an early paromomyid primate (Mammalia). Science, N.Y. 184:903-905 (1974).

COOPER, C. FORSTER: On the ear region of certain of the Chrysochloridae. Phil. Trans. R. Soc. Lond. B216:265-281 (1928).

CORBET, G.B. and HANKS, J.: A revision of the elephant-shrews, family Macroscelididae. Bull. br. Mus. nat. Hist. Zool. 16:5-111 (1968).

CORSY, F.: Évolution de l'appareil hyo-branchial (P. Ciafra, Marseille 1933).

DALLOS, P.: Low-frequency auditory characteristics: species dependence. J. acoust. Soc. Am. 48:489-499 (1970).

DALLOS, P.: The auditory periphery. (Academic Press, London 1973).

DANIEL, P.M.; DAWES, J.D.K., and PRICHARD, M.M.L.: Studies of the carotid rete and its associated arteries. Phil. Trans. R. Soc. Lond. B237:173-204 (1953).

DAVIES, D.V.: Gray's anatomy, descriptive and applied; 34th ed. (Longmans, London 1967).

DAVIES, D.V. and DAVIES, F.: Gray's anatomy, descriptive and applied; 33rd ed. (Longmans, London 1962).

DAVIS, D.D.: Comparative anatomy and the evolution of the vertebrates; in G.L. JEPSEN, E. MAYR and G.G. SIMPSON Genetics, paleontology and evolution, pp. 64-89 (Atheneum, N.Y. 1963; reprint of 1949 ed.).

DE BEER, G.R.: *vide* BEER, G.R. DE.

DE LA TORRE, E. and NETSKY, M.G.: *vide* TORRE, E. DE LA and NETSKY, M.G.

DENE, H.; GOODMAN, M.; PRYCHODKO, W., and MOORE, G.W.: Immunodiffusion systematics of the primates. III. The Strepsirhini. Folia primatol. 25:35-61 (1976).

DIAMANT, M.: Otitis and pneumatization of the mastoid bone. Acta oto-laryngol., suppl. 41, pp. 1-149 (1940).

DU BOULAY, G.H. and VERITY, P.M.: *vide* BOULAY, G.H. DU and VERITY, P.M.

ELLERMAN, J.R.; MORRISON-SCOTT, T.C.S., and HAYMAN, R.W.: Southern African mammals 1758 to 1951: a reclassification (British Museum, London 1953).

ELOFF, F.C.: The homology of the mammalian pterygoid in the light of some new evidence. Proc. Linn. Soc. Lond. 162:56-63 (1950).

EVANS, F.G.: The osteology and relationships of the elephant shrews (Macroscelididae). Bull. am. Mus. nat. Hist. 80:85-125 (1942).

FAWCETT, E.: The primordial cranium of *Erinaceus europaeus*. J. Anat. 52:211-250 (1918).

FAWCETT, E.: The primordial cranium of *Miniopterus schreibersi* at the 17 millimetre total length stage. J. Anat. 53:315-350 (1919).

ENLOW, D.H.: A study of the post-natal growth and remodelling of bone. Am. J. Anat. 110:79-101 (1962).

FIEDLER, W.: Übersicht über das System der Primaten; in H. HOFER, A.H. SCHULTZ, and D. STARCK Primatologia, vol. 1, pp. 1-266 (Karger, Basel 1956).

FINDLAY, G.H.: The development of the auditory ossicles in the elephant shrew, the tenrec and the golden mole. Proc. zool. Soc. Lond. 1944:91-99 (1944).

FLEISCHER, G.: Studien am Skelett des Gehörorgans der Säugertiere, einschliesslich des Menschen. Saugetierk. Mitt. 21:131-239 (1973).

FLOWER, W.H.: On the value of the characters of the base of the cranium in the classification of the order Carnivora, and on the systematic position of *Bassaris* and other disputed forms. Proc. zool. Soc. Lond. 1869:4-37 (1869).

FORSTER, A.: L'inclinaison du tympan chez les mammifères supérieurs et chez l'homme. Arch. Anat. Histol. Embryol. 4:295-321 (1925).

FORSTER COOPER, C.: *vide* COOPER, C. FORSTER.

FORSYTH MAJOR, C.I.: *vide* MAJOR, C.I. FORSYTH.

FREI, H.: Das Primordialcranium eines Fetus von *Avahis laniger*; med. Diss. Bern (1938).

FRICK, H.: Zur Morphogenese der Fenestra rotunda. Verh. Anat. Ges. (50. Versamml., Marburg):194-203 (1952).

FRICK, H.: Die Entwicklung und Morphologie des Chondrokraniums von Myotis (Beitrag zur Kenntnis der Morphologie und Entwicklung des Chiropterkraniums III) (Georg Thieme, Stuttgart 1954).

GASC, J.P.: Sur une fenestration de la base du crâne chez les espèces de petite taille du genre Suncus Ehrenburg. Mammalia 27:81-91 (1963).

GAUNT, W.A.: Microreconstruction (Pitman, London 1971).

GAUPP, E.: Beitränge zur Morphologie des Schädels. III. Zur vergleichenden Anatomie der Schläfengegend am knöchernen Wirbelthier-Schädel. Morphol. Arb. 4:77-128 (1895).

GAUPP, E.: Das Chondrocranium von Lacerta agilis. Ein Beitrag zum Verständnis des Amniotenschädels. Anat. Hefte 14:433-439 (1900).

GAUPP, E.: Neue Deutungen auf dem Gebiete der Lehre vom Saugetierschadel. Anat. Anz. 27:273-310 (1905).

GAWNE, C.E.: The genus Proterix (Insectivora, Erinaceidae) of the upper Oligocene of North America. Am. Mus. Novit. 2315:1-26 (1968).

GETTY, R.: The ear; in M.E. MILLER, G.C. CHRISTENSEN and H.E. EVANS Anatomy of the dog, pp. 847-863 (Saunders, Philadelphia 1964).

GILLETTE, R.G.; BROWN, R.; HERMAN, P.; VERNON, S., and VERNON, J.: The auditory sensitivity of the lemur. Am. J. phys. Anthropol. 38:365-370 (1973).

GINGERICH, P.D.: Anatomy of the temporal bone in the Oligocene anthropoid Apidium and the origin of Anthropoidea. Folia primatol. 19:329-337 (1973).

GINGERICH, P.D.: Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). Univ. Michigan Pap. Paleontol. 15:1-141 (1976).

GOODMAN, M.: Protein sequence and immunological specificity: their role in phylogenetic studies of primates; in W.P. LUCKETT and F.S. SZALAY Phylogeny of the primates, a multidisciplinary approach, pp. 219-248 (Plenum Press, N.Y. 1975).

GOODRICH, E.S.: Studies on the structure and development of vertebrates (Macmillan, London 1930).

GOULD, S.J.: Ontogeny and the explanation of form: an allometric analysis. J. Paleontol. 42:81-98 (1968).

GREGORY, W.K.: The orders of mammals. Bull. am. Mus. nat. Hist. *27*:3-524 (1910).

GREGORY, W.K.: I. On the relationship of the Eocene lemur *Notharctus* to the Adapidae and to other primates. II. On the classification and phylogeny of the Lemuroidea. Bull. geol. Soc. Am. *26*:419-446 (1915).

GREGORY, W.K.: On the structure and relations of *Notharctus*, an American Eocene primate. Mem. am. Mus. nat. Hist. *3*:49-243 (1920).

GROVES, C.P.: Taxonomy and phylogeny of prosimians; in R.D. MARTIN, G.A. DOYLE and A.C. WALKER Prosimian biology, pp. 449-473 (Duckworth, London 1974).

GUTH, C.; HEIM DE BALSAC, H., and LAMOTTE, M.: Recherches sur la morphologie de *Micropotamogale lamottei* et l'évolution des Potamogalinae. I. Ecologie, denture, anatomie crânienne. Mammalia *23*:423-447 (1959).

HAECKEL, E.: Generelle Morphologie der Organismen (Reimer, Berlin 1866).

HAINES, R.W. and MOHUIDDIN, A.: Metaplastic bone. J. Anat. *103*:527-538 (1968).

HALL, B.K.: A histochemical study of the condylar secondary cartilage of the mouse, *Mus musculus* (Mammalia:Rodentia). Aust. J. Zool. *16*:807-813 (1968).

HEFFNER, H.; RAVIZZA, R., and MASTERTON, B.: Hearing in primitive mammals. III. Tree shrew (*Tupaia glis*). J. aud. Res. *9*:12-18 (1969).

HENCKEL, K.O.: Zur Entwicklungsgeschichte des Halbaffenschädels. Z. Morphol. Anthropol. *26*:365-383 (1927).

HENCKEL, K.O.: Studien über das Primordialcranium und die Stammesgeschichte der Primaten. Morphol. Jahrb. *59*:105-178 (1928).

HENSON, O.W.: Some morphological and functional aspects of certain structures of the middle ear in bats and insectivores. Univ. Kansas Sci. Bull. *42*:151-255 (1961).

HERSHKOVITZ, P.: The ectotympanic bone and origin of higher primates. Folia primatol. *22*:237-242 (1974).

HIGBEE, D.: Functional anatomy of the autonomic nervous system; in G.M. ENGLISH Otolaryngology, vol. 3, ch. 21a, pp. 1-16 (Harper & Row, Hagerstown 1975).

HILL, W.C.O.: Primates: comparative anatomy and taxonomy. I. Strepsirhini (Edinburgh University Press, Edinburgh 1953).

HINCHCLIFFE, R. and PYE, A.: Variations in the middle ear of the Mammalia. J. Zool., Lond. 157:277-288 (1969).

HOLLARD, M.H.: Du temporal et des pièces qui en représentent les éléments dans la série des animaux vertébrés. Ann. Sci. nat. Zool. Biol. anim. 1:359-376 (1864). [Cited in VAN DER KLAAUW 1922.]

HOYTE, D.A.N.: The postnatal growth of the ear capsule in the rabbit. Am. J. Anat. 108:1-16 (1961).

HOYTE, D.A.N.: Experimental investigations of skull morphology and growth. Int. Rev. Gen. Exp. Zool. 2:345-407 (1966).

HUNT, R.M.: The auditory bulla in Carnivora: an anatomical basis for reappraisal of carnivore evolution. J. Morphol. 143:21-76 (1974).

HYRTL, J.: Vergleichend-anatomische Untersuchungen über das innere Gehörorgan des Menschen und der Säugethiere (Prague, 1845). [Cited in GREGORY 1910.]

HYRTL, J.: Zur vergleichended Anatomie der Trommelhöhle. Denkschr. kais. Acad. Wiss., Wien (1850). [Cited in VAN KAMPEN 1905.]

JOHNSTON, T.B.; DAVIES, D.V., and DAVIES, F.: Gray's anatomy, descriptive and applied; 32nd ed. (Longmans, London 1958).

JONES, F. WOOD and LAMBERT, V.F.: The occurrence of the lemurine form of the ectotympanic in a primitive marsupial. J. Anat. 74: 72-72 (1939).

KAMPEN, P.N. VAN: Die Tympanalgegend des Säugetierschädels. Morphol. Jahrb. 34:321-722 (1905).

KAMPEN, P.N. VAN: De phylogenie van het entotympanicum. Tijds. nederl. dierk. Ver. 14:24-36 (1915).

KANAGASUNTHERAM, R. and KANAN, C.F.: The chondrocranium of a 19 mm C.R. length embryo of *Galago senegalensis senegalensis*. Acta zool., Stockh. 45:107-121 (1964).

KANAGASUNTHERAM, R. and KRISHNAMURTI, A.: Observations on the carotid rete in the lesser busy baby (*Galago senegalensis senegalensis*). J. Anat. 99:861-875 (1965).

KEEN, J.A. and GROBBELAAR, C.S.: The comparative anatomy of the tympanic bulla and auditory ossicles, with a note suggesting their function. Trans. R. Soc. S. Afr. 28:307-329 (1941).

KERMACK, K.A. and KIELAN-JAWOROWSKA, Z.: Therian and non-therian mammals; in D.M. KERMACK and K.A. KERMACK Early mammals, Zool. J. Linn. Soc. Lond. 50:suppl. 1, pp. 103-115 (Academic Press, London 1971).

KIELAN-JAWOROWSKA, Z.: Unknown structures in multituberculate skull. Nature, Lond. 226:974-976 (1970).

KIELAN-JAWOROWSKA, Z.: Preliminary description of two new eutherian genera from the late Cretaceous of Mongolia; in Z. KIELAN-JAWOROWSKA Results of the Polish-Mongolian Palaeontological Expeditions--Part VI, Palaeontol. Pol. 33:5-15 (1975).

KEIBEL, F.: The development of the sense-organs; in F. KEIBEL and F.P. MALL Manual of human embryology, vol. 2, pp. 180-290 (Lippincott, Philadelphia 1912).

KLAAUW, C.J. VAN DER: Über die Entwickelung des Entotympanicums. Tijds. nederl. dierk. Ver. 18:135-174 (1922).

KLAAUW, C.J. VAN DER: Die Skelettstücken in der Sehne des musculus stapedius und nahe dem Ursprung der Chorda tympani. Z. Anat. Entwicklungsgesch. 69:32-83 (1923).

KLAAUW, C.J. VAN DER: On the development of the tympanic region of the skull in the Macroscelididae. Proc. zool. Soc. Lond. 1929: 491-560 (1929).

KLAAUW, C.J. VAN DER: On mammalian auditory bullae showing an indistinct complex structure in the adult. J. Mammal. 11:55-60 (1930).

KLAAUW, C.J. VAN DER: The auditory bulla in some fossil mammals, with a general introduction to this region of the skull. Bull. am. Mus. nat. Hist. 62:1-352 (1931).

KOSKINEN, L.; ISOTUPA, K., and KOSKI, K.: A note on craniofacial growth. Am. J. phys. Anthropol. 45:511-516 (1976).

KÖSTLIN, O.: Der Bau des knöchernen Kopfes in den vier Klassen der Wirbelthiere (Stuttgart 1844). [Cited in VAN KAMPEN 1905.]

KRISHNAMURTI, A.: The cerebral arteries of Nycticebus coucang coucang. Folia primatol. 8:159-168 (1968).

KÜHN, H.-J.: Die Entwicklung und Morphologie des Schädels von Tachyglossus aculateus. Abh. Senckenb. Naturforsch. Ges. 528: 1-224 (1971).

LAMBERTON, C.: Contribution à la connaissance de la faune subfossile de Madagascar. Note IX. Oreille osseuse des lémuriens. Mém. Acad. Malgache 35:1-132 (1941).

LAY, D.M.: The anatomy, physiology, functional significance and evolution of specialized hearing organs of gerbilline rodents. J. Morphol. 138:41-120 (1972).

LECHE, W.: Über die Säugethiergattung Galeopithecus. Kongl. svenska Vetensk. Akad. Handl. 21(11):1-92 (1885).

LECHE, W.: Zur Entwicklungsgeschichte des Zahnsystems der Säugethiere. Thiel II: Phylogenie. Heft I: Die Familie der Erinaceidae. Zoologica, Stuttg. 37:1-103 (1902.

LE GROS CLARK, W.E.: vide CLARK, W.E. LE GROS.

LEIMGRUBER, C.: Le crâne primordial d'un embryon de Centetes ecaudatus. Biomorphosis 1:545-585 (1939).

LUCKETT, W.P.: Comparative development and evolution of the placenta in primates; in W.P. LUCKETT Reproductive biology of the primates, Contrib. primatol. 3:142-234 (1974).

LYON, M.W.: Tree shrews: an account of the mammalian family Tupaiidae. Proc. U.S. natl Mus. 45:1-188 (1913).

MACINTYRE, G.T.: The trisulcate petrosal pattern of mammals; in T. DOBZHANSKY, M.K. HECHT and W.C. STEERE Evolutionary biology, vol. 6, pp. 275-303 (Appleton-Century-Crofts, N.Y. 1972).

MACPHEE, R.D.E.: Ontogeny of the ectotympanic-petrosal plate relationship in strepsirhine prosimians. Folia primatol. 27:245-283 (1977).

MAJOR, C.I. FORSYTH: Exhibition of, and remarks upon, some skulls of fetal Malagasy lemurs. Proc. zool. Soc. Lond. 1899:987-988 (1899).

MARTIN, R.D.: Reproduction and ontogeny in tree shrews (Tupaia belangeri), with reference to their general behavior and taxonomic relationships. Z. Tierpsychol. 25:409-532 (1968a).

MARTIN, R.D.: Towards a new definition of primates. Man 3:377-401 (1968b).

MASTERTON, B.; HEFFNER, H., and RAVIZZA, R.: The evolution of human hearing. J. acous. Soc. Am. 45:966-985 (1969).

MCCRADY, E.: The embryology of the oppossum. Am. Anat. Mem. 16: 1-233 (1938).

MCDOWELL, S.B.: The Greater Antillean insectivores. Bull. am. Mus. nat. Hist. 115:113-214 (1958).

MCKENNA, M.C.: New evidence against the tupaioid affinities of the mammalian family Anagalidae. Am. Mus. Novit. 2158:1-16 (1963).

MCKENNA, M.C.: Paleontology and the origin of the primates. Folia primatol. 4:1-25 (1966).

MCKENNA, M.C.: Toward a phylogenetic classification of the Mammalia; in W.P. LUCKETT and F.S. SZALAY Phylogeny of the primates, a multidisciplinary approach, pp. 21-46 (Plenum Press, N.Y. 1975).

MEISTER, W. and DAVIS, D.D.: Placentation of the pigmy tree shrew (Tupaia minor). Fieldiana Zool. 35:71-84 (1956).

MØLLER, A.R.: The middle ear; in P.V. TOBIAS Foundations of modern auditory theory, vol. 2, pp. 133-194 (Academic Press, N.Y. 1972).

MOFFETT, B.C.: A research perspective on craniofacial morphogenesis. Acta morphol. neerl. -scand. 10:91-101 (1972).

MOSS, M.L.: Growth of the calvaria in the rat. Am. J. Anat. 94: 333-362 (1954).

MOSS, M.L.: Fusion of the frontal suture in the rat. Am. J. Anat. 102:141-165 (1958).

MOSS, M.L.: Inhibition and stimulation of sutural fusion in the rat calvaria. Anat. Rec. 136:457-468 (1960).

MOSS, M.L.: Ontogenetic aspects of cranio-facial growth; in R.E. MOYERS and W.M. KROGMAN Cranio-facial growth in man, pp. 109-124 (Pergamon Press, Oxford 1971).

MURRAY, P.D.F.: Cartilage and bone: a problem in tissue differentiation. Aust. J. Sci. 14:65-73 (1957).

NAPIER, J.R. and NAPIER, P.H.: A handbook of living primates. (Academic Press, London 1967).

OAKS, E.C.: Structure and function of inflated middle ears of rodents; PhD Diss. Yale (1967).

OJALA, L.: Contribution to the physiology and pathology of mastoid air-cell formation: histological studies of aged individuals and newborn infants. Acta oto-laryngol., suppl. 86, pp. 1-134 (1950).

OJALA, L.: Pneumatization of the bone and environmental factors: experimental studies on chick humerus. Acta oto-laryngol., suppl. 133, pp. 1-28 (1957).

OPHEIM, O.: The pneumatic conditions of the human temporal bone in the light of experimental researches on the development of the air space in the chick humerus. Acta oto-laryngol., suppl. 54, pp. 1-116 (1944).

PADGET, D.H.: The development of the cranial arteries in the human embryo. Contrib. Embryol. Carnegie Inst., no. 212, 32:205-261 (1948).

PARKER, W.K.: On the structure and development of the skull in Mammalia. Part III. Insectivora. Phil. Trans. R. Soc. Lond. 176:121-275 (1886).

PATTERSON, B.: The fossil elephant shrews (family Macroscelididae). Bull. Mus. comp. Zool., Harv. Coll. 133:295-335 (1965).

PEARSON, A.A. and JACOBSON, A.D.: The development of the ear (American Academy of Ophthalmology and Otolaryngology, Rochester 1967).

PETERS, W.C.H.: Naturwissenchaftliche Reise nach Mossambique. Zoologie. I. Säugethiere (Berlin 1842). [Cited in VAN DER KLAAUW 1929.]

PRITCHARD, J.J.; SCOTT, J.H., and GIRGIS, F.G.: The structure and development of cranial and facial sutures. J. Anat. 90:73-86 (1956).

PROCTOR, B.: Embryology and anatomy of the eustachian tube. Arch. Otolaryngol. 86:503-514 (1967).

PUSEY, H.K.: Methods of reconstruction from microscopic sections. J.R. microsc. Soc. 59:232-244 (1939).

PYE, A. and HINCHCLIFFE,R.: Structural variations in the mammalian middle ear. Med. biol. Illus. 18:122-127 (1968).

RAMASWAMI, L.S.: The development of the skull in the slender loris, Loris tardigradus lydekkerianus Cabr. Acta zool., Stockh. 38:27-68 (1957).

REINBACH, W.: Zur Entwicklung des Primordialcraniums von Dasypus novemcinctus Linné (Tatusia novemcincta Lesson) II. Z. Morphol. Anthropol. 45:1-72 (1952).

RICH, T.H.V. and RICH, P.V.: Brachyerix, a Miocene hedgehog from western North America, with a description of the tympanic regions of Paraechinus and Podogymnura. Am. Mus. Novit. 2477:1-58 (1971).

RICHANY, S.F.; ANSON, B.J., and BAST, T.H.: The ear and the temporal bone, development and adult structure; in G.M. ENGLISH Otolaryngology, vol. 1, ch. 1, pp. 1-140 (Harper & Row, Hagerstown 1975).

ROUX, G.H.: The cranial development of certain Ethiopian 'insectivores' and its bearing on the mutual affinities of the group. Acta zool., Stockh. 28:165-397 (1947).

RUËDI, L.: Die Mittelohrraumentwicklung vom 5. Embryonalmonat bis zum 10. Lebensjahr. Acta oto-laryngol., suppl. 22, pp. 1-134 (1937).

RUGH, R.: A guide to vertebrate development; 6th ed. (Burgess, Minneapolis 1971).

RUSSELL, D.E.: Les mammifères paléocenes d'Europe. Mém. Mus. natl Hist. nat., Paris, Sér. C 13:1-321 (1964).

SABAN, R.: Phylogénie des insectivores. Bull. Mus. natl Hist. nat., Paris, ser. 2 26:419-432 (1954).

SABAN, R.: Les affinités du genre Tupaia Raffles 1821, d'après les caractères morphologiques de la tête osseuse. Ann. Paléontol. 42: 169-224 (1956); 43:1-44 (1957).

SABAN, R.: Contribution à l'étude de l'os temporal des primates. Description chez l'homme et les prosimiens. Anatomie comparée et phylogénie. Mém. Mus. natl Hist. nat., Paris, Ser. A 29: 1-378 (1963).

SABAN, R.: Sur la pneumatisation de l'os temporal des Primates adultes et son développement ontogenique chez le genre Alouatta (Platyrhinien). Morphol. Jahrb. 106:569-593 (1964).

SCHNEIDER, R.: Zur Entwicklung des Chondrocraniums der Gattung Bradypus. Morphol. Jahrb. 95:210-301 (1955).

SEGALL, W.: The middle ear region of Dromicipos. Acta anat. 72: 489-501 (1969a).

SEGALL, W.: The auditory ossicles (malleus, incus) and their relationships to the tympanic: in marsupials. Acta anat. 73:176-191 (1969b).

SEGALL, W.: Morphological parallelisms of the bulla and auditory ossicles in some insectivores and marsupials. Fieldiana Zool. 51:169-205 (1970).

SEPPÄLÄ, A.J.: Variations in the pneumatic cell system of the temporal bone: acute otitis media and complications in varying types of pneumatisation. Acta. oto-laryngol., suppl. 64, pp. 1-131 (1946).

SICHER, H. and S.N. BHASKAR: Orban's oral histology and embryology; 7th ed. (Mosby, Saint Louis 1972).

SIMONETTA, A.: Anatomia e significato morfologico e sistematico dell' orecchio medio e delle strutture ad esso connesse in alcuni insettivori (Suncus, Talpa, Chrysochloris). Arch. ital. Anat. Embriol. 62:55-94 (1957a).

SIMONETTA, A.: Sull'esistenza digiunti cinetici nel cranio di alcuni insettivori (Myosorex, Talpa) e sul loro possibile significato. Monit. zool. ital. 64:172-180 (1957b).

SIMONETTA, A.: Condrocranio e dermascheletro di "Chrysochloris asiatica" (Linnaeus). Monit. zool. ital. 65:28-47 (1957c).

SIMONETTA, A.: Cranial kinesis and the morphology of the middle ear: two possibly related features. Evolution 17:580-587 (1963).

SIMONS, E.L.: Primate evolution, an introduction to man's place in nature (Macmillan, N.Y. 1972).

SIMONS, E.L.: Notes on early Tertiary prosimians; in R.D. MARTIN, G.A. DOYLE, and A.C. WALKER Prosimian biology, pp. 415-433 (Duckworth, London 1974).

SIMPSON, G.G.: The major features of evolution (Simon & Schuster, N.Y. 1953).

SIMPSON, G.G.: Primate taxonomy and recent studies of nonhuman primates. Ann. N.Y. Acad. Sci. 102:497-514 (1962).

SISSON, S.: The anatomy of the domestic animals; 3rd ed., rev. by J.D. GROSSMAN (Saunders, Philadelphia 1938).

SPATZ, W.B.: Beitrang zur Kenntnis der Ontogenese des Cranium von Tupaia glis (Diard 1820). Morphol. Jahrb. 106:321-416 (1964).

SPATZ, W.B.: Zur Ontogenese der Bulla tympanica von Tupaia glis Diard 1820 (Prosimiae, Tupaiiformes). Folia primatol. 4:26-50 (1966).

SPRAGUE, J.M.: The hyoid region in the Insectivora. Am. J. Anat. 74:175-216 (1944).

STADTMÜLLER, F.: Kranium und Visceralskelett der Säugetiere; in L. BOLK, E. GÖPPERT, E. KALLIUS, and W. LUBOSCH Handbuch der vergleichenden Anatomie der Wirbeltiere, vol. 4, pp. 839-1016 (Urban & Schwartzenburg, Berlin 1936).

STARCK, D.: Zur Morphologie des Primordialcraniums von Manis javanica Desm. Morphol. Jahrb. 86:1-122 (1941).

STARCK, D.: Das Cranium eines Schimpansenfetus (Pan troglodytes [Blumenbach 1799]) von 71 mm SchStlg., nebst Bemerkungen über die Körperform von Schimpansenfeten (Beitrag zur Kenntnis des Primatencraniums II). Morphol. Jahrb. 100:599-647 (1960).

STARCK, D.: Das Cranium von Propithecus spec. (Prosimiae, Lemuriformes, Indriidae) (Beiträge zur Kenntnis des Primaten-Craniums III). Bibl. primatol., vol. 1, pp. 163-196 (1962).

STARCK, D.: Über das Entotympanicum der Canidae und Ursidae (Mammalia, Carnivora, Fissipeda). Acta theriol. 8:181-188 (1964).

STARCK, D.: Embryologie, ein Lehrbuch auf allgemein biologischer Grundlage; 2nd ed. (Georg Thieme, Stuttgart 1965).

STARCK, D.: Le crâne des mammifères; in P. GRASSÉ Traité de zoologie, vol. 16, part 1, pp. 405-549, 1095-1102 (Masson, Paris 1967).

STARCK, D.: The development of the chondrocranium in primates; in W.P. LUCKETT and F.S. SZALAY Phylogeny of the primates, a multidisciplinary approach, pp. 127-155 (Plenum Press, N.Y. 1975).

STEHLIN, H.G.: Die Säugetiere des schweizerischen Eocaens. Siebenter Teil, erste Hälfte. Adapis. Abh. schweiz. paläont. Ges. 38: 1165-1298 (1912).

STEPHAN, H.: Bericht über eine belgisch-deutsche Gemeinschaftsexpedition in Belgish-Kongo. Mitt. Max-Planck-Ges. 2:96-106 (1958).

STEPHAN, H.: Forschungsreise nach Lemuria (Madagaskar). Mitt. Max-Planck-Ges. 5:318-333 (1963).

STEUERWALD, E.A.: Review of the phylogenetic position on the tree shrew (Tupaia glis Diard), with new observations on the arteria carotis interna; PhD Diss. Michigan State (1969).

STORY, H.E.: The carotid arteries in the Procyonidae. Fieldiana Zool. 32:477-557 (1951).

SZALAY, F.S.: The beginnings of primates Evolution 22:19-36 (1968).

SZALAY, F.S.: Mixodectidae, Microsyopidae, and the insectivore-primate transition. Bull. am. Mus. nat. Hist. 140:193-330 (1969).

SZALAY, F.S.: Cranial morphology of the early Tertiary Phenacolemur and its bearing on primate phylogeny. Am. J. phys. Anthropol. 36:59-76 (1972a).

SZALAY, F.S.: The paleobiology of the earliest primates; in R. TUTTLE The functional and evolutionary biology of primates, pp. 3-35 (Aldine, Chicago 1972b).

SZALAY, F.S.: Phylogeny of primate higher taxa: the basicranial evidence; in W.P. LUCKETT and F.S. SZALAY Phylogeny of the primates, a multidisciplinary approach, pp. 91-125 (Plenum Press, N.Y. 1975).

SZALAY, F.S.: Systematics of the Omomyidae (Tarsiiformes, Primates): taxonomy, phylogeny, and adaptations. Bull. am. Mus. nat. Hist. 156:157-450 (1976).

SZALAY, F.S. and KATZ, C.: Phylogeny of lemurs, galagos and lorises. Folia primatol. 19:88-103 (1973).

TANDLER, J.: Zur vergleichenden Anatomie der Kopfarterien bei den Mammalia. Denkschr. kais. Acad. Wiss., Wien 67:677-784 (1899).

TANDLER, J.: Zur Entwicklungsgeschichte der Kopfarterien bei den Mammalia. Morphol. Jahrb. 30:275-373 (1902).

TATTERSALL, I. and SCHWARTZ, J.H.: Craniodental morphology and the systematics of the Malagasy lemurs (Primates, Prosimii). Anthropol. Pap. am. Mus. nat. Hist. 52:139-192 (1974).

THOMAS, O. and SCHWANN, H.: The Rudd exploration of South Africa. V. List of mammals obtained by Mr. Grant in N.E. Transvaal. Proc. zool. Soc. Lond. 1906:575-591 (1906).

TONNDORF, J. and KHANNA, S.M.: The quality of impedance matching by the middle ears of cats. Ann. Otol. Rhinol. Laryngol. 77:154-163 (1968).

TORRE, E. DE LA and NETSKY, M.G.: Study of persistent primitive maxillary artery in human fetus: some homologies of cranial arteries in man and dog. Am. J. Anat. 106:185-195 (1960).

VALEN, L. VAN: Tree shrews, primates and fossils. Evolution 19: 137-151 (1965).

VALEN, L. VAN: New Paleocene Insectivora and insectivore classification. Bull. am. Mus. nat. Hist. 135:217-284 (1967).

VAN DER KLAAUW, C.J.: vide KLAAUW, C.J. VAN DER.

VAN KAMPEN, P.N.: vide KAMPEN, P.N. VAN.

VAN VALEN, L.: vide VALEN, L. VAN.

VERSLUYS, J.: Die mittlere und äussere Ohrsphäre der Lacertilia und Rhynchocephalia. Zool. Jahrb., Abt. Anat. Ontog. 12:161-406 (1898). [Cited in VAN DER KLAAUW 1922.]

WALKER, A.C.: A review of the Miocene Lorisidae of East Africa; in R.D. MARTIN, G.A. DOYLE and A.C. WALKER Prosimian biology, pp. 435-447 (Duckworth, London 1974).

WALKER, E.P.; WARNICK, F.; LANGE, K.I.; UIBLE, H.E.; HAMLET, S.E.; DAVIS, M.A., and WRIGHT, P.F.: Mammals of the world; 3 vols. (Johns Hopkins, Baltimore 1964).

WASSIF, K.: Studies on the structure of the auditory ossicles and tympanic bone in Egyptian Insectivora, Chiroptera, and Rodentia. Bull. Fac. Sci. Fouad I Univ. 27:177-213 (1948).

WEBER, M.: Die Säugetiere. Einführung in die Anatomie und Systematik der recenten und fossilen Mammalia; 2nd ed., 2 vols. (Fischer, Jena 1927-28).

WEBSTER, D.B.: The ear apparatus of the kangeroo rat, Dipodomys. Am. J. Anat. 108:123-148 (1961).

WEBSTER, D.B.: A function of the enlarged middle ear cavities of the kangeroo rat, Dipodomys. Physiol. Zool. 35:248-255 (1962).

WEBSTER, D.B.: Ear structure and function in modern mammals. Am. Zool. **6**:451-466 (1966).

WEBSTER, D.B.: Auditory systems of Heteromyidae: postnatal development of the ear of *Dipodomys merriami*. J. Morphol. **146**:377-394 (1975).

WEBSTER, D.B. and STROTHER, W.F.: Middle ear morphology and auditory sensitivity of heteromyid rodents. Am. Zool. **12**:727 (1972).

WEBSTER, D.B. and WEBSTER, M.: Auditory systems of Heteromyidae: functional morphology and evolution of the middle ear. J. Morphol. **146**:343-376 (1975).

WEGNER, R.N.: Die Paukeninnenbeine (Endotympanicum und Epipterygoid) bei den Säugetieren. Photographie und Forschung **3**:289-303 (1942).

WEIDENREICH, F.: Das Knochengewebe; in W. VON MOLLENDORFF Handbuch der mikroscopischen Anatomie des Menschen, vol. 2, pp. 391-508 (Springer, Berlin 1930).

WEINMANN, J.P. and SICHER, H.: Bone and bones: fundamentals of bone biology; 2nd ed. (Mosby, Saint Louis 1955).

WERNER, C.F.: Das Mittel- und Innenohr; in H. HOFER, A.H. SCHULTZ and D. STARCK Primatologia, vol. 2, Teil 1, Lieferung 5, pp. 1-40 (Karger, Basel 1960a).

WERNER, C.F.: Das Gehörorgan der Wirbeltiere und des Menschen. Beispiel für eine vergleichende Morphologie der Lagesbeziehungen (VEB Georg Thieme, Leipzig 1960b).

WIŃCZA, H.: O niektórych zmianach rozwoju w okolicy osady głowy u zwierząt ssących. (Über einige Entwickelungsveränderungen in der Gegend des Schädelgrundes bei den Säugethieren). Bull. int. Acad. Sci. Cracovie **1896**:326-337 (1896).

WINGE, H.: Jordfundne og nulevende Flagermus (Chiroptera) fra Lagoa Santa, Minas Geraes, Brasilien. Med Udsigt øver Flagermusenes indbyrdes Slaegtskab. E Museo Lundii **2**(1):1-92 (1892). [Trans. by E. DIECHMANN and G.M. ALLEN appears in A.S. JENSEN, R. SPÄRCK and H. VØLSOE The interrelationships of the mammalian genera, vol. 1, Monotremata, Marsupialia, Insectivora, Chiroptera, Edentata (Reitzels, København 1941).]

WINGE, H.: Jordfundne og nulevende Aber (Primates) fra Lagoa Santa, Minas Geraes, Brasilien. Med Udsigt øver Abernes indbyrdes Slaegtskab. E Museo Lundii **2**(2):1-57 (1895). [Trans. by E. DIECHMANN and G.M. ALLEN appears in A.S. JENSEN, R. SPÄRCK and H. VØLSOE The interrelationships of the mammalian genera, vol. 2, Rodentia, Carnivora, Primates (Reitzels, København 1941).]

WOOD JONES, F. and LAMBERT, V.F.: *vide* JONES, F. WOOD and LAMBERT, V.F.

WÜNSCH, D.: Zur Kenntnis der Entwicklung des Craniums des Koboldmaki, *Tarsius bancanus borneanus*, Horsfield, 1821 (Beiträge zur Kenntnis des Primaten-Craniums IV) (Selbstverlag Sencken. Anat. Inst., J.-W.-Goethe-Univ., Frankfurt/M 1975).

YUODELIS, R.H.: The morphogenesis of the human temporomandibular joint and its associated structures. J. dent. Res. **45**:182-191 (1966).

APPENDICES

APPENDIX I

GENERAL FUNCTION OF THE MIDDLE EAR

The chief function of the middle ear is to transmit air-borne vibrations received by the tympanic membrane in such a way that they become strong enough to move the fluids of the internal ear. It does so by transforming the low-pressure, high-amplitude sound waves carried by the air into waves which are of smaller amplitude but of correspondingly greater pressure. The necessity for this transformation of acoustical energy is related to the air-water boundary problem. Air and water (or any other fluid) differ greatly in their compressibility and density, and hence in their characteristics for transmitting acoustical energy (technically described as their acoustic impedances). The middle ear matches these impedances, or in less complex terms, overcomes the opposition to energy flow.

Mechanically, transformation is accomplished in two ways. The force striking the tympanic membrane is concentrated into the far smaller footplate of the stapes, which has the effect of increasing the force per unit area (pressure). Secondly, the ossicular chain has leverage, which also has the effect of increasing pressure at the footplate.

This analysis is not complete, however, because it does not consider the energy dissipated or stored by the biological transformer and its associated structures. Stated in another way, the middle ear exerts its own influence on the flow of energy, i.e., has its own impedance.

Energy flow in any mechanical system is affected by factors of friction, mass, and stiffness. The first factor (the 'resistive' component) is minimal in the case of the middle ear because the articulations of the delicately-suspended ossicles are normally enclosed in joint capsules. The other two, however, are important. Mass and stiffness are called the 'reactive' component of acoustic impedance, since they store energy. In doing so they reduce the overall efficiency of the middle ear mechanism by diverting part of the energy flow into potential energy. Mass is contributed by the tympanic membrane and ossicular chain. Stiffness is produced by many agencies, including the tension of the tympanic membrane, ossicular ligaments, anular legament of the fenestra vestibuli, tonus of the ossicular muscles and the volume of air enclosed within the middle ear.

Mass and stiffness stand in a specific, reciprocal relationship: mass reactance increases and stiffness reactance decreases with increasing frequency. Total reactance is the difference between mass and stiffness factors; but because the relationship is reciprocal, these two factors will cancel each other at some point in the frequency spectrum. This point is the resonant frequency, and at this frequency the transfer of acoustic energy is at its maximum. Experiments on several mammals establish that the resonant frequencies predicted by theoretical considerations actually correspond with the most sensitive frequency of these animals (DALLOS 1970; WEBSTER and WEBSTER 1975).

Middle ear morphology can affect the reactance offered by both the mass and stiffness factors. Alteration in either will also affect the position of the resonant frequency. If mass is great, sensitivity will be reduced for frequencies above the area of greatest sensitivity; if stiffness is great, sensitivity will be reduced for frequencies below the area of greatest sensitivity. Further, reduction of either factor will promote an increased degree of sensitivity above or below the resonant frequency.

APPENDIX II

DEFINITIONS

The first duty of the morphologist to his readers is clarity of description, and fundamental to the accomplishment of this duty is the proper and consistent use of anatomical terms. Structurally, the mammalian auditory region is one of the more complex parts of the body, and to describe it adequately one requires a similarly elaborate terminology.

In order to save the reader unnecessary labor, I have assembled a comprehensive glossary of anatomical terms which should considerably ease the task of visualizing the positions and relations of structures described in the text.

I have attempted to follow what I think is the most logical course regarding usage. First, I have chosen, in most instances, the English equivalents of names officially recognized by *Nomina anatomica* (third ed., 1966), *Nomina anatomica veterinaria* (first ed., 1968), and *Nomina embryologica* (first ed., June 1970 revision). (These are abbreviated in the text as NA, NAV, and NE, respectively.) Secondly, in cases where no official name was available for a structure which is otherwise well-known, I have selected what I believe to be the *au courant* term in the literature. Thirdly, in cases where structures have not been previously recognized, or where a recognized term is for one good reason or another inadequate, I have fashioned my own names. Finally, I have also listed, where appropriate, common synonyms of the chosen names. Listed Latin names are usually, but not always, those recognized by the Nominae.

Generally speaking, the definitions accompanying each of the terms are paraphrases of definitions or descriptions in well-known works with good illustrations. These works are cited next to the corresponding definitions. Inverted commas indicate a direct quote. In other cases, the following convention is used. If the stated definition departs in only minor ways from an original source, only author, date and page number are listed. If the departure includes major alterations in phraseology or meaning, reference data are preceded by the verb "see". In several instances, suitably lucid or complete definitions could not be found, and I have coined my own.

ALA TEMPORALIS

A lateral appendage of the central stem which usually chondrifies independently, but which soon fuses to the processus alaris. It forms a considerable part of the floor of the cavum epiptericum, which lodges the trigeminal ganglion. (DE BEER 1929:453-454.)

In mammals, it is the representative of the processus ascendens of the pterygoquadrate cartilage, and therefore part of the visceral arch skeleton, which in phylogeny was completely distinct in origin from the processus alaris. (DE BEER 1937:450.)

ALICOCHLEAR COMMISSURE
(ANTERIOR TRABECULO-COCHLEAR COMMISSURE)

The transitory, cartilaginous bridge which joins the anterior pole of pars cochlearis to the processus alaris of the central stem. It forms the lateral border of the foramen caroticum primitivum, separating it from the piriform fenestra. (See DE BEER 1929:414.)

Although normally present in fetal mammals, its development may be so retarded that it completely fails to appear in the young stages of some forms (e.g., Loris, Galago). It usually disappears through resorption or de-differentiation, although ossification may extend into the commissure and so produce the lingula sphenoidale (case in Homo).

ALISPHENOID

A bone of the skull which contributes to the basicranium, orbit and other areas. It arises within the ala temporalis, although most of its growth is accomplished by intramembranous (periosteal) ossification. Fuses with the pterygoid and basisphenoid. (See DE BEER 1937:369-370.)

AN(N)ULUS MEMBRANE

According to some authors (e.g., VAN KAMPEN 1905; SABAN 1956-57, 1963), a special membrane which fastens the ventral rim of the ectotympanic to the internal aspect of the lateral bullar wall in certain mammals (e.g., tree shrews, lemurs).

In fact, the anulus membrane does not exist, at least as an entity separate from the tissues of the membranous meatus and the tunica mucosa of the tympanic cavity.

AN(N)ULUS TYMPANICUS

See ECTOTYMPANIC.

ANTERIOR BASICAPSULAR COMMISSURE
(SPHENOCOCHLEAR COMMISSURE)

The transitory, cartilaginous bridge which joins the anteromedial side of pars cochlearis to the basal plate of the central stem. It forms the anterior border of the basicapsular fenestra as well as the posterior border of the foramen caroticum primitivum. (See STARCK 1967:444.)

It is not constant, and in cases (or stages) where it is absent the basicapsular fenestra communicates with the foramen caroticum primitivum.

ANTERIOR CAROTID ARTERY
(CAROTIDE ANTÉRIEURE, ?ASCENDING PHARYNGEAL A., A. FORAMINIS LACERI, APPARENT INTERNAL CAROTID A.)

The large vessel found in strepsirhines which arises from the common carotid and which supplies most of the extravertebral arterial blood destined for the brain. Unlike the internal carotid, it does not enter the tympanic cavity, but instead travels outside it. The artery reaches the circulus arteriosus through the anterior carotid foramen. In lorises, the vessel bears a rete mirabile of simple structure.

CARTMILL (1975:324) believes that the anterior carotid is the homologue of the ascending pharyngeal artery of Homo and many other mammals. It is unlikely to be the medial carotid artery, since both the medial carotid and ascending pharyngeal artery are present in some mammals (e.g., carnivores).

ANTERIOR CAROTID FORAMEN

The bony foramen (or canal) of the osteocranium through which the promontorial artery (or the joint vessel formed by the anastomosis of the promontorial and anterior carotid or ascending pharyngeal or medial carotid) actually enters the cranial cavity. It is the ontogenetic successor of the foramen caroticum primitivum (q.v.) of the chondrocranium.

Various bones may participate in the bounding of this foramen, especially when it is prolonged into a canal. Further, it is sometimes confluent with the piriform fenestra. However, basisphenoidal material inevitably lies at least on the medial side of the intracranial aperture of the anterior carotid foramen, for the artery passing through the foramen emerges medial or slightly posteromedial to the position of the hypophysis.

This term is preferred to foramen lacerum medium, a term which has lost its valency because it is used in so many different ways. It should also be noted that a single foramen does not always succeed the foramen caroticum primitivum. Adult mammals sometimes have separate foramina in the base of the skull for the promontorial artery and anterior carotid (or medial carotid), or a separate foramen for veins draining intracranial sinuses. (See STORY 1951:513.)

ANTEROMEDIAL PROCESS (OF THE BULLA)
(PROCESSUS ANTEROMEDIALIS)

The moderately-inflated projection of the auditory bulla which lies on or points towards the basioccipital-basisphenoidal synchondrosis, medial to the tubal canal. (See VAN DER KLAAUW 1931:118.)

APERTURA (FOSSULAE) FENESTRAE VESTIBULI
(APERTURA FENESTRAE OVALIS)

"The vestibular window...is a transversely oval opening in the outer wall of the otic capsule; in the fresh state the fenestra is closed by the base of the stapes and the annular ligament" (RICHANY, ANSON and BAST 1975:104).

Unlike the fenestra cochleae (q.v.), the fenestra vestibuli is not deeply recessed within the auditory capsule. However, a fossula fenestrae vestibuli is named in the NA.

APERTURA FOSSULAE FENESTRAE COCHLEAE
(APERTURA FOSSULAE FENESTRAE ROTUNDAE)

The entrance to a diverticulum of the middle ear (the fossula fenestrae cochleae, q.v.) within which the secondary tympanic membrane is situated. It conforms to the "fenestra cochleae" (or "rotunda") of earlier authors who believed that the secondary tympanic membrane lay across the apertura itself. (See FRICK 1952.)

See also FOSSULA FENESTRAE COCHLEAE, FENESTRA COCHLEAE.

APERTURA LATERALIS OF THE RECESSUS SCALAE TYMPANI

The aperture of the cartilaginous otic capsule which is completed ventrally by the processus recessus and which becomes the fenestra cochleae of the osteocranium. (DE BEER 1929:461-466).

APERTURA MEDIALIS OF THE RECESSUS SCALAE TYMPANI

An aperture of the cartilaginous otic capsule which conducts the perilymphatic duct into the cranial cavity and which is completed ventrally by the processus recessus. This opening becomes the cochlear canaliculus after the ossification of the capsule. (DE BEER 1929:461-466.)

AQUEDUCTUS COCHLEAE

See COCHLEAR CANALICULUS

ARTERY OF THE PTERYGOID CANAL
(A. CANALIS PTERYGOIDEI, VIDIAN A.)

The artery which accompanies the nerves of the pterygoid canal through the passageway of the same name (see PTERYGOID CANAL). It is usually of insignificant size in recent mammals, and extremely variable in its connexions. However, it is probably an ancient branch of the mammalian carotid system (see VAN VALEN 1966:9-10; SZALAY 1975: 94-95), and is still an important collateral channel between the internal and external carotids in some mammals (see DE LA TORRE and NETSKY 1960).

At least in Homo, the artery of the pterygoid canal represents a persistent remnant of the primitive mandibular artery (first aortic arch). It is initially connected to the developing internal carotid, but later it is taken over by the (internal) maxillary artery of the external carotid. In most adult humans, it appears as a branch of the third or pterygopalatine division of the maxillary artery and is distributed to the pharynx and the auditory tube. Occasionally, the initial embryonic connexion will remain and the artery will arise instead from the intrapetrous portion of the internal carotid. (See PADGET 1948.)

The connexion with the internal carotid, which may well be primitive for mammals, is found in some lipotyphlans (e.g., Erinaceus europaeus). (See fig. I-4.)

AUDITORY or OTIC CAPSULE

"...is divisible into two portions. One is postero-dorsal in position and lodges the utricle and semicircular canals, forming the canalicular part [pars canalicularis] of the auditory capsule. The other is anteroventral in position, and accommodates the ductus cochlearis of the saccule, forming the cochlear capsule [pars cochlearis]" (DE BEER 1929:416).

AUDITORY OSSICLES

The malleus, incus and stapes. The malleus and incus derive from the material of both the first and second visceral bars, while the stapes derives from the second visceral bar (crura and head) and the material of the otic capsule (footplate or base). In addition, the anterior process of the malleus partly derives from an independent element, the gonial (q.v.). (See PEARSON and JACOBSON 1967:16-42.)

AUDITORY REGION

As used here, a locative term (such as "face", "valut", "jaws") for the part of the basicranium which contains the vestibulocochlear organ and the elements which enclose or lie immediately adjacent to it. More specifically, it includes the petrosal and the contiguous parts of the bones or cartilages which contact or lie near the petrosal (usually, the squamosal, alisphenoid, basisphenoid, exoccipital, basioccipital, proximal part of the hyoid apperatus [Reichert's cartilage], ectotympanic, cartilage of the auditory tube, incus, stapes, malleus gonial, Meckel's cartilage, pterygoid and, among the inconstant elements, the entotympanic[s], element of Spence and of Paaw).

AUDITORY TUBE
(TUBA AUDITIVA, EUSTACHIAN TUBE, PHARYNOGOTYMPANIC TUBE)

The channel of communication between the tympanic cavity (cavum tympani) and the pharynx. The tube is lined by a mucous membrane which is continuous with that of the tympanic cavity at one end (tympanic ostium), and with that of the nasopharynx at the other (pharyngeal ostium).

The endoderm of the primitive pharynx forms an endodermal pouch by pressing outward toward the ectoderm at the site of the corresponding branchial groove. The groove, situated between the first (mandibular) and second (hyoid) arches and supported, respectively, by Meckel's and Reichert's cartilages, becomes (in part) the elongate auditory tube. (See ANSON and DONALDSON 1973:21, 173.)

AURICLE
(AURICULA, PINNA)

The outer part of the external ear. (ANSON and DONALDSON 1973:30.)

AURICULAR CARTILAGE
(CARTILAGO AURICULAE, CARTILAGE OF THE PINNA)

The elastic cartilage of complicated shape which forms the essential support of the external ear. It is a derivative of the mesoderm of the first branchial arch. (ANSON and DONALDSON 1973:18.)

Although the anular cartilage (or cartilage of the external acoustic meatus) forms separately and is not part of the auricular cartilage _per se_ (see GETTY 1964:850), no attempt is made to distinguish the two in the figures.

AURICULAR RAMUS OF THE VAGUS NERVE
(RAMUS AURICULARIS N. VAGI, N. OF ARNOLD)

The nerve, containing somatic afferent fibers, which is released by the proximal (or jugular) ganglion of the vagus in the posterior lacerate foramen. It runs laterally across the mastoid region to the site of the stylomastoid foramen, where it joins or distributes filaments to the facial nerve. The nerve continues onwards to ramify in the integument of the external ear. (See SISSON 1938:826.)

See also MASTOID CANALICULUS.

BASAL PLATE

See CENTRAL STEM.

BASICAPSULAR FENESTRA
(BASICOCHLEAR FISSURE)

"...a space included between the ventromedial edge of the auditory capsule and the lateral edge of the parachordal cartilage [basal plate]" (DE BEER 1937:399). It is bounded by the anterior and posterior basicapsular commissures (if present).

In some cases (e.g., most soricomorphs; MCDOWELL 1958:202), this fenestra is not completely obliterated in the adult, which results in the basicranial exposure of part of the inferior petrosal sinus (q.v.).

BASILAR ARTERY
(A. BASILARIS)

So named from its position at the base of the cranial cavity. The artery is formed by the junction of the two vertebral arteries, which are in turn branches of the subclavian. Anteriorly, the basilar artery divides into the two posterior cerebral arteries, which communicate with the circulus arteriosus (q.v.). (JOHNSTON et al. 1958:769.)

BASISPHENOID BONE
(OS BASISPHENOIDALE)

One of the endochondral bones of the basicranium. It arises from paired centers in the cartilage of the central stem which become fused together and with another pair of ossification centers which arise subsequently in the processus alaris. The latter, or alar, centers extend backwards in the alicochlear commissures thus giving rise to the lingulae sphenoidales (conditions in Homo; DE BEER 1937: 370.)

The basisphenoid eventually meets the alisphenoid as they expand towards each other in the degenerating processus alaris. In the forms considered here, their fusion is complete and no suture separates them in the adult. Other fusions of relevance here include those with the posterior part of the pterygoid bone (usually early) and with the basioccipital at the site of the basioccipital-basisphenoidal synchondrosis (usually late, sometimes never completed).

BRANCHIAL ARCHES
(VISCERAL ARCHES, PHARYNGEAL ARCHES)

The six pairs of mesodermal masses between the branchial pouches and lateral to the pharynx of all vertebrate embryos. Each arch is bounded by the endoderm on the pharyngeal side and the ectoderm on the outside. (RUCH 1971:349.)

The mesoderm of each arch is pluripotential, and, in addition to certain other structures, typically gives rise to an aortic arch, a skeletal element, and muscles (true of the first three arches, which are the only ones of interest here). The skeletogenic mesoderm of an arch is here separately denoted as a visceral bar (q.v.). Derivatives of the first three arches and their associated ecto- and endoderm are listed in Table 1-2.

BRANCHIAL CLEFTS
(VISCERAL CLEFTS, GROOVES)

The set of furrows (usually only three or four prominent ones in mammals) which externally bound the (first three or four) branchial arches. They are produced by the invagination of the ectoderm, and either meet or come into close relation with the corresponding branchial pouches leading from the primitive pharynx. (See BAXTER 1953:206-218.)

In mammals, all except the first cleft (located between the first and second branchial arches), which helps form the external acoustic meatus, normally disappear. (DAVIES 1967:147.)

BRANCHIAL POUCHES
(VISCERAL POUCHES, PHARYNGEAL POUCHES)

The set of indentations (usually five in mammals) of the primitive pharynx, produced by the evagination of its endoderm, which internally bound the branchial arches. (See BAXTER 1953:206-218.)

The tympanic cavity and auditory tube are derived from the first and possibly the second branchial pouches. (BAST and ANSON 1949:306-307.)

CANALICULUS FOR THE CHORDA TYMPANI
(CANALICULUS CHORDAE TYMPANI)

See CHORDA TYMPANI.

CARTILAGE OF THE AUDITORY TUBE
(CARTILAGO TUBAE AUDITIVAE)

The channelled, elongated piece of elastic cartilage which conducts the auditory tube towards the tympanic cavity. It often appears crook-or staff-shaped in cross-section. Of uncertain derivation.

CAUDAL CHORDAFORTSATZ

The bony or cartilaginous process which conducts the chorda tympani from its point of entry into the tympanic cavity towards the malleus. It may develop from the ectotympanic, petrosal, or Reichert's cartilage, or it may form independently and later fuse to one or another of these elements. (See BONDY 1907:400-401.)

A Chordafortsatz which forms independently is distinguished as an element of Spence (q.v.).

CAUDAL ENTOTYMPANIC

An entotympanic which arises in the rear part of the ventral wall of the middle ear, often in proximity to Reichert's cartilage.

See ENTOTYMPANIC(S).

CAUDAL TYMPANIC PROCESS OF THE PETROSAL
(PROCESSUS TYMPANICUS PETROSI CAUDALIS)

As used here, any tympanic process which arises primarily from the ventral surface of the mastoid region of pars canalicularis.

It usually makes its first appearance as a cartilaginous ridge which grows outwards from, or is closely related to, the walls of the apertura fossulae fenestrae cochleae. In some cases (lemurs, lorises), the posterior continuation of the crista parotica is involved in its production as well.

In the forms considered here, it apparently never has its own center of ossification, but ossifies in continuity with the rest of the petrosal.

See PETROSAL PLATE.

CAVERNOUS SINUS

The large dural sinus, situated on either side of the sella turcica, through which the promontorial (or cerebral carotid) artery passes on its way to the circulus arteriosus. (See JOHNSTON *et al.*, 1958:850.)

CAVUM SUPRACOCHLEARE

The space on the dorsal (cerebral) surface of the auditory capsule which houses the geniculate ganglion of the facial nerve. In the fetus it is bounded by the suprafacial commissures. The greater petrosal nerve and filaments destined for the tympanic plexus and the lesser petrosal nerve are given off by the geniculate in the cavum supracochleare. (See DE BEER 1937:430.)

In the adult, the cavum is recessed within the internal acoustic meatus. However, bone does not completely cover this space, for it remains open anteriorly at the hiatus of the facial canal (q.v.).

CAVUM TYMPANI

As used here, the sac bounded by mucous membrane which fills (in the adult) the (presumptive) tympanic cavity.

See TYMPANIC CAVITY and section 1.4.1.

CENTRAL STEM

In older embryos and fetuses, the bar or plate of fused cartilages which extends from the tip of the nose to the foramen magnum. It arises from three sources: the trabecular plate (or cartilago trabecularis, forming the nasal septum), the hypophyseal plate (or cartilago hypophysealis, surrounding the hypophyseal stalk), and the basal plate (or cartilago parachordalis, through which the notochord passes). In the prenatal stages relevant to this study, the three are more or less indistinguishably fused and will be collectively referred to as the central stem. (See ROUX 1947:175-176.)

Ossifications of interest here whose centers appear in the central stem or its outgrowths are the basisphenoid (initially in the hypophyseal plate), the basioccipital (initially in the posterior part of the basal plate), and the exoccipitals (initially in the occipital arches or cartilago occipitalis, which usually chondrify from the posterolateral angles of the basal plate). (See STARCK 1967:438.)

CHORDA TYMPANI

The mixed nerve released by the facial nerve beneath the stylomastoid foramen (see fig. I-4). It passes into the middle ear between the posterior crus of the ectotympanic and (usually) the squamosal; its foramen of entry may be well-defined and bony, in which case a canaliculus chordae tympani may be identified. Or, it may simply pass through the fibrous tissue related to the pars flaccida of the tympanic membrane, which fills the gap between the ectotympanic and the squamosal.

It passes around the medial surface of the malleus in close relation to the area of insertion of the tensor tympani, then runs alone the malleolar sulcus of the ectotympanic in company with the gonial (which it often perforates). The nerve emerges from the tympanic cavity through the Glaserian fissure.

Most of its fibers are afferent from the mucous membrane of the anterior two-thirds of the tongue. It also contains secretomotor fibers destined for the submandibular ganglion. (See DAVIES and DAVIES 1962:1138.)

CIRCULUS ARTERIOSUS
(CIRCLE OF WILLIS)

"...formed at the interpeduncular space of the base of the brain by the union of the anterior cerebral arteries in front, by the diverging posterior cerebral arteries behind, and is completed laterally by the junction of the latter with the posterior communicating arteries and by the internal carotid [i.e., promontorial branch of the internal carotid]". (SISSON 1938:653.)

COCHLEAR CANALICULUS
(CANALICULUS COCHLEAE)

The small canal which establishes communication between the scala tympani and the subarachnoid space, and which transmits the perilymphatic duct. Its intracranial aperture lies directly behind and below the internal acoustic meatus, and is sometimes visible from the ventral aspect by looking through the posterior lacerate foramen. (See ANSON and DONALDSON 1973:187.)

In the NA, 'aqueductus cochleae' is considered to be an official alternative for the perilymphatic duct. However, it should be noted that the 'aqueductus cochleae' of older works almost always refers to the cochlear canaliculus.

CRISTA PAROTICA

In mammalian fetuses the crista parotica has the form of a downward and backward sloping ledge on the lateral side of the auditory capsule which accentuates the prominence of the lateral semicircular canal and forms the lateral wall of the (cartilaginous) facial sulcus. The tegmen tympani develops as an anteriorly-directed projection on the middle portion of the crista parotica, while Reichert's cartilage normally fuses with its lateral portion. (DE BEER 1937:405.)

The crista parotica is typically continued backwards for a distance behind the place where it fuses with Reichert's cartilage. This part of the crista parotica, which is sometimes involved in the production of a part of the caudal tympanic process of the petrosal, is here separately denoted as the "posterior continuation of the crista parotica". In the adult, the (now ossified) posterior continuation is often visible as a low ridge behind the root of the tympanohyal (in cases where it is not incorporated into a true caudal tympanic process of the petrosal).

CRISTA TYMPANICA

The low semicircular ridge (actually the dorsal margin of the ectotympanic) which borders the tympanic sulcus. (BONDY 1907:300.)

DEEP PETROSAL NERVE
(N. PETROSUS PROFUNDUS)

This nerve may be thought of as the continuation of the lateral branch (or plexus) of the internal carotid nerve to the lacrimal gland and nasal mucosa. Here, it will be considered to start where the lateral of the internal carotid nerve comes into close relation with the greater petrosal nerve on the roof of the tympanic cavity, beneath the piriform fenestra (see fig. I-4). The deep petrosal and greater petrosal nerves continue forwards as the nerves of the pterygoid canal (q.v.). (See DAVIES 1967:1250.)

DIVERTICULUM

As used here, a general term for any well-marked fossa or recess on the walls of the middle ear, other than those with common names (e.g., epitympanic recess, fossula fenestrae cochleae, fossa for the tensor tympani).

ECTOTYMPANIC
(AN[N]ULUS TYMPANICUS, TYMPANIC RING, TYMPANIC BONE)

The intramembranous bone which supports the tympanic membrane. (MCDOWELL 1958:129.)

Embryonically, it always has the form of a horseshoe, being incomplete dorsolaterally at the tympanic notch. It may be said to consist of two legs, termed here the anterior and posterior crura.

The ectotympanic develops within connective tissue surrounding the developing tympanic membrane, sometimes from multiple centers (e.g., Homo). (See RICHANY, BAST and ANSON 1975:9.)

ELEMENT OF PAAW (or PAAUW)

A small piece of bone or cartilage which is found in the tendon of the stapedius muscle in some mammals. (HENSON 1961:163.)

It may be a vestige of the extrastapes (extracolumella) of reptiles (VAN DER KLAAUW 1923; DE BEER 1937:441), or the functional equivalent of a sesamoid bone (MCCRADY 1938). However, whatever its evolutionary roots, in modern mammals it must be considered an ontogenetic derivative of the interhyal, the transitory bridge of blasteme which initially connects the stapes primordium to the rest of the second visceral (hyoid) bar and which becomes the tendon of the stapedius muscle (case in Homo). (See PEARSON and JACOBSON 1967:26.)

Spelling (Paaw rather than the usual Paauw) is that recommended by HINCHCLIFFE and PYE (1969:279).

ELEMENT OF SPENCE

An inconstant skeletal element which lies in the rear of the tympanic cavity, immediately in front of the origin of the chorda tympani from the facial nerve, and a short distance from the anterior aspect of Reichert's cartilage. When large, it extends medially to the position of the malleus, thereby forming a supporting strut for the chorda tympani in this part of its route. In many cases it apparently remains partly or wholly cartilaginous, while in others it ossifies. It may secondarily fuse to other elements (e.g., squamosal, ectotympanic). (VAN DER KLAAUW 1923:622.)

The element of Spence, like the element of Paaw (q.v.), may represent a vestige of the reptilian extrastapes (extracolumella). However, the relationship of the element of Spence to the chorda tympani and malleus suggests that in the modern mammal the first-named structure is a derivative of the so-called "interbranchial bridge" which connects the first (mandibular) to the second (hyoid) visceral bar, and which gives rise to part of the malleus and incus (case in Homo). (See PEARSON and JACOBSON 1967:20.)

ENTOGLENOID PROCESS OF THE SQUAMOSAL

A descending part of the squamosal which is of interest here because it may, in some mammals, incidentally bound the anterolateral part of the tympanic cavity. In some mammals it functionally replaces the processus postglenoideus as the articular eminence for the mandible. See fig. I-2. (See MCDOWELL 1958:123.)

ENTOTYMPANIC(S)
(OS ENTOTYMPANICUM, TUBOTYMPANIC, ENDOTYMPANIC, METATYMPANIC)

"Under this name we take together all the skeletal elements, bony or cartilaginous, that lie in the ventral wall of the tympanic cavity and are ontogenetically primarily independent of the other elements in the auditory bulla, except perhaps the tympanohyal and the cartilage of the Eustachian tube" (VAN DER KLAAUW 1931:266).

Sometimes two (or even more) separate entotympanics can be distinguished, in which case rostral and caudal elements are identified.

See ROSTRAL ENTOTYMPANIC, CAUDAL ENTOTYMPANIC.

EPITYMPANIC CREST

A term coined here to refer to the incomplete septum which borders the anterior margin of the epitympanic recess in lorises and lemurs (and perhaps other mammals as well). The stapedial artery either penetrates or travels in a bony canal along this crest; the crest is not a Chordafortsatz (q.v.) and has no relationship with the chorda tympani.

EPITYMPANIC RECESS
(RECESSUS EPITYMPANICUS, ATTICUS TYMPANICUS)

The epitympanic recess is a dorsal extension of the tympanic cavity which lies above the upper level of the tympanic membrane. Contained within it are those parts of the malleus and incus which articulate to form the incudomalleolar articulation. (HENSON 1961:156.)

"The recessus epitympanicus is covered on the medial side by the tegmen tympani of the periotic, which is also a neomorph in mammals, also by the squamosal, while the lateral part is very differently developed" (VAN DER KLAAUW 1931:73).

EPITYMPANIC WING

A general term used for any bony or cartilaginous horizontal outgrowth of a basicranial bone which contributes to the roof of the middle ear.

See TYMPANIC PROCESS and fig. I-3.

EPITYMPANIC WING OF THE SPHENOID

On of the epitympanic wings commonly found in the anterior part of the roof of the tympanic cavity. Often, both the alisphenoid and the basisphenoid participate in this wing, but their separate contributions cannot be made out in the adult because of fusion.

See fig. I-3.

EPITYMPANIC WING OF THE PETROSAL

A term coined here to refer to the (usually) small anterodorsal outgrowth of the pars cochlearis which forms part of the roof of the tympanic cavity in some mammals. It is originally independent of the tegmen tympani (q.v.), although the two may fuse together later in ontogeny. This epitympanic wing is often, but not always, associated with a large rostral tympanic process of the petrosal.

See fig. I-3.

EPITYMPANIC WING OF THE SQUAMOSAL

The medial extension of the squamosal which participates in the roof of the tympanic cavity in the area of the epitympanic recess. Very small or deficient in some forms.

See fig. I-3.

EXTERNAL ACOUSTIC MEATUS
(MEATUS ACUSTICUS EXTERNUS)

In the living mammal, the channel which extends from the bottom of the auricle to the tympanic membrane. It consists of a cartilaginous portion (formed by the auricular cartilage) and an osseous portion (usually formed by the ectotympanic, although sometimes by the petrosal or entotympanic). Covering both these portions and lining the entire lumen is the skin of the external acoustic meatus (also known as the membranous meatus).

There is considerable variation among mammals in the degree to which the osseous portion is built outwards. (See VAN KAMPEN 1905: 358-359.)

EXTERNAL EAR

The auricle and external acoustic meatus.

FACIAL CANAL
(CANALIS FACIALIS)

See FACIAL SULCUS.

FACIAL (VII) NERVE
(N. FACIALIS)

The nerve of the second (hyoid) visceral arch. From its superficial origin at the lateral part of the corpus trapezoideum to its foramen of exit from the cranium (stylomastoid foramen), it follows a tortuous course through the auditory capsule.

In the fetal mammal, it passes into the presumptive tympanic cavity by means of the foramen faciale (q.v.) after traversing the cavum supracochleare, entering slightly above and in front of the apertura fenestrae vestibuli. It then bends posteriorly and ventrally on the lateral wall of pars canalicularis (labyrinthine wall), beneath the root of the tegmen tympani. It leaves the middle ear by passing around the posterior face of Reichert's cartilage, through the foramen stylomastoideum primitivum (q.v.). (See STARCK 1965:429.)

See fig. I-4.

FACIAL SULCUS (or CANAL)
(SULCUS FACIALIS, CANALIS FACIALIS)

The sulcus is the groove which accommodates the facial nerve in its passage through the tympanic cavity. Usually, it can be traced from the foramen faciale to the stylomastoid foramen. (See DE BEER 1929:418.)

The facial nerve is never enclosed in a complete cartilaginous tube during ontogeny, although in many species periosteal outgrowths of the ossifying petrosal may eventually enclose the nerve in a canal (facial canal, aqueduct of Fallopius). (See STARCK 1965:428.)

FENESTRA COCHLEAE
(COCHLEAR FENESTRA, FENESTRA ROTUNDA, ROUND WINDOW)

"The cochlear fenestra...lies in the anterosuperior wall of the fossula. Its bony margin is formed posteriorly by part of the cochlear capsule, inferiorly by bone developed in late fetal life from a related bar of cartilage [processus recessus], anteriorly by part of the inner portion of the bony promontory, and superiorly by the two bony spiral laminas....In a macerated specimen the window opens into the cochlea; in the fresh state it is closed by the secondary tympanic membrane" (RICHANY, ANSON and BAST 1975:95-96).

See FOSSULA FENESTRAE COCHLEAE.

FENESTRA VESTIBULI
(FENESTRA OVALIS, OVAL WINDOW)

See APERTURA FENESTRAE VESTIBULI.

FIBROUS MEMBRANE OF THE TYMPANIC CAVITY

The connective-tissue membrane which ventrally encloses, and forms the original floor of, the presumptive tympanic cavity.

See section 1.4.1.

FISSURA METOTICA

An aperture of the chondrocranium situated between the basal plate medially, the occipital posteriorly, and the auditory capsule laterally. It is closed anteriorly by the fusion of the medial wall of the auditory capsule with the edge of the basal plate. (DE BEER 1929:414.)

The internal jugular vein and the IX, X and XI cranial nerves pass through the fissura metotica to their various destinations. In later ontogeny, the fissura is often subdivided by cartilage or bone into a jugular foramen and a foramen for the cranial nerves.

See POSTERIOR LACERATE FORAMEN.

FORAMEN CAROTICUM PRIMITIVUM

Restricted here to the foramen of the chondrocranium through which the promontorial artery enters the cranial cavity. This foramen has certain constant relations to other basicranial structures:

"...the processus alaris (basitrabecular process) develops just in front of where the carotid enters the skull. Behind the carotid is the cochlear part of the auditory capsule, but the carotid is still free laterally and not enclosed until the alicochlear commissure develops, joining the ala temporalis with the pars cochlearis. This encloses the carotid in a foramen caroticum..." (DE BEER 1926:342).

The alicochlear commissure does not always develop, and for cases where this occurs an incisura carotica primitiva is distinguished. Later in ontogeny, the cartilaginous foramen caroticum primitivum becomes the bony anterior carotid foramen (q.v.) as a result of the growth of surrounding bones.

FORAMEN FACIALE
(APERTURA TYMPANICA CANALIS FACIALIS)

As used here, the foramen through which the facial nerve enters the middle ear from the cavum supracochleare. (See DE BEER 1929:418.)

This foramen is sometimes (and incorrectly) called the foramen stylomastoideum primitivum (q.v.).

FORAMEN FOR THE GREATER PETROSAL NERVE

A remnant of the piriform fenestra (in species in which the fenestra is obliterated), by means of which the greater petrosal nerve enters the tympanic cavity.

On the dorsal surface of the auditory capsule, this foramen is joined to the hiatus of the facial canal (q.v.) by means of a short furrow (the sulcus for the greater petrosal nerve).

FORAMEN FOR THE LESSER PETROSAL NERVE
(CANALICULUS INNOMINATUS)

Used in those cases where the lesser petrosal nerve passes through an aperture in the tympanic process of the alisphenoid which is separate from the foramen for the ramus inferior of the stapedial artery (q.v.).

FORAMEN FOR THE RAMUS INFERIOR (OF THE STAPEDIAL ARTERY)

The foramen (or notch) in the tympanic process of the alisphenoid, adjacent to the foramen ovale, which transmits the ramus inferior. (GREGORY 1920:172.)

This foramen often transmits the lesser petrosal nerve and small veins as well.

FORAMEN FOR THE RAMUS SUPERIOR (OF THE STAPEDIAL ARTERY)

The foramen in the roof of the tympanic cavity through which the ramus superior and accompanying veins escape into the cranial cavity. It usually lies in the tegmen tympani, or between the latter and the epitympanic wings of the squamosal and the sphenoid (i.e., in part of the piriform fenestra).

This term is used in preference to foramen spinosum, the aperture through which the middle meningeal artery enters the cranial cavity in Homo. Although the human middle meningeal is partly derived from the embryonic stapedial system, its development in man and certain other higher primates is so specialized (see BUGGE 1974) that it seems better to employ a generalized term for describing conditions in other mammals.

FORAMEN OVALE

"The foramen ovale always looks toward the inner face of the mandible, since it gives exit to the mandibular branch of the trigeminal nerve" (GREGORY 1910:429.)

The foramen ovale usually lies entirely within the alisphenoid.

FORAMEN STYLOMASTOIDEUM DEFINITIVUM

See STYLOMASTOID FORAMEN.

FORAMEN STYLOMASTOIDEUM PRIMITIVUM

See STYLOMASTOID FORAMEN.

FOSSA FOR THE STAPEDIUS MUSCLE
(FOSSA MUSCULARIS MINOR)

The shallow depression which accommodates the origin of the stapedius muscle. It lies posteromedial to the stylomastoid foramen and tympanohyal and posterolateral to the apertura fossulae fenestrae cochleae. (MACINTYRE 1972:282-282.)

FOSSA FOR THE TENSOR TYMPANI MUSCLE
(FOSSA MUSCULARIS MAJOR)

The shallow depression which accommodates the belly and a small part of the origin of the tensor tympani. It lies on the upper part of pars cochlearis, or on the latter and the epitympanic wing of the petrosal.

FOSSA INCUDIS

"...a small depression in the lower and posterior part of the epitympanic recess; it lodges the short process of the incus, which is fixed to the fossa by ligamentous fibers" (DAVIES 1967:1322).

FOSSULA FENESTRAE COCHLEAE
(FOSSULA FENESTRAE ROTUNDAE, PELVIS ROTUNDA)

The funnel-shaped niche in the auditory capsule which contains the fenestra cochlea and hides it from view.

"The fossula...is an irregularly prismatic recess, with rounded angles, which extends from a point near the bottom of the middle ear upward and inward beneath the arch of the first turn of the cochlea. One surface of the prism-shaped space is directed downward and represents the tympanic aditus [apertura] of the fossula. Much of the rim of the opening is formed by the overhanging ledge of the promontory produced by the arch of the first coil of the cochlea" (RICHANY, ANSON and BAST 1975:92).

See APERTURA FOSSULAE FENESTRAE COCHLEAE, FENESTRA COCHLEAE.

GLASERIAN FISSURE
(FISSURA GLASERI, FISSURA PETROTYMPANICA)

"...is at first the aperture for the cartilage of Meckel, which disappears later in the development. Later on we find the chorda tympani in it and often also the ramus inferior of the stapedial artery.

"The fissura Glaseri lies between: (a) the sulcus malleolaris of the tympanic...and (b) the periotic, or (c) the margo fissurae of the squamosal...; it lies alongside the tegmen tympani" (VAN DER KLAAUW 1931:164).

The entotympanic can also be involved, as in Tupaia.

Although an eponymous name, "Glaserian fissure" is preferable to the "fissura petrotympanica" of the NA, for the latter term is not descriptive of conditions in many non-human forms.

GLOSSOPHARYNGEAL (IX) NERVE
(N. GLOSSOPHARYNGEUS)

The cranial nerve issuing from the posterior lacerate foramen (see fig. I-4) which supplies motor fibers to muscles of the pharynx and the parotid gland, and sensory fibers to the pharynx, tonsil and posterior part of the tongue. (JOHNSTON et al., 1958:1127.)

GONIAL
(GONIALE, PREARTICULAR)

An intramembranous ossification of mammals which fuses with the malleus (and occasionally the ectotympanic as well) and which forms part of the processus anterior (gracilis, Folii of adult Homo). It is usually perforated or notched by the chorda tympani. (DE BEER 1937:441.)

GREATER PETROSAL NERVE
(N. PETROSUS MAJOR, GREATER SUPERFICIAL PETROSAL N., PALATINE BRANCH OF THE FACIAL N.)

A branch of communication of the facial nerve (geniculate ganglion to pterygopalatine ganglion) which consists chiefly of sensory branches which are distributed to the mucous membrane of the soft palate; but it also contains the preganglionic fibers which form the motor root of pterygopalatine ganglion.

From its origin at the geniculate ganglion the nerve passes through the hiatus of the facial canal, runs along the cerebral surface of the auditory capsule beneath the trigeminal ganglion, and meets the deep petrosal nerve by travelling through the piriform fenestra (or its own foramen) into the middle ear. The greater and deep petrosal nerves travel in close relation thereafter, as the nerves of the pterygoid canal (fig. I-4). (See DAVIES 1967:1160.)

HIATUS OF THE FACIAL CANAL
(HIATUS CANALIS FACIALIS, HIATUS FALLOPII)

The foramen on the anterodorsal surface of the petrosal, leading from the cavum supracochleare, through which escape the greater petrosal nerve and filaments destined for the tympanic plexus and lesser petrosal nerve. (See ANSON and DONALDSON 1973:5.)

HYPOGLOSSAL FORAMEN or CANAL

The foramen in the occipital for the hypoglossal (XII) nerve. The names "condylar foramen" and "condyloid foramen" are not used here, because of the possible confusion with the condyloid canal for a vein. (MCDOWELL 1958:125.)

HYPOTYMPANIC SINUS
(SINUS HYPOTYMPANICUS)

"The hypotympanic sinus covers a part of the tympanic cavity that contains none of its principal elements, including the auditory ossicles and the fenestrae in the periotic. It is formed when the ventral wall loses its flatness and becomes inflated on the medial or caudal side" (VAN DER KLAAUW 1931:19).

INFERIOR PETROSAL SINUS
(SINUS PETROSUS INFERIOR)

A vein of the dura mater, draining from the cavernous sinus to the internal jugular. (DAVIES 1967:897.)

In man, its route is entirely intracranial and it meets the internal jugular within the jugular foramen. In some mammals, however, the distal section of the sinus is partly exposed between the petrosal and the basioccipital, and the place where it meets the internal jugular may be extracranial (i.e., beneath rather than within the jugular foramen or posterior lacerate foramen). This exposure is due to the failure of the basicapsular fenestra to close during the ossification of the cranium.

INTERNAL CAROTID ARTERY
(A. CAROTIS INTERNA, ENTOCAROTID A.)

A division of the common carotid artery which (usually) provides the greater part of the arterial supply of the anterior part of the brain, the eye and its appendages. However, in numerous mammals this vessel may be partly or wholly obliterated during ontogeny. (See BUGGE 1974.)

The internal carotid is considered here to terminate at the point where it bifurcates into the stapedial and promontorial arteries (see fig. I-4).

INTERNAL CAROTID NERVE
(N. CAROTICUS INTERNUS)

This nerve originates from the cranial (or superior) cervical ganglion of the autonomic nervous system and contains postganglionic fibers. It ascends the internal carotid artery and enters the posterior carotid foramen in company with the latter vessel. Just before or after it passes through the foramen, the nerve divides,usually into a lateral and a medial branch. Both branches then follow the promontorial artery, after the bifurcation of the internal carotid artery, towards the anterior pole of the promontory (see fig. I-4).

The internal carotid nerve communicates with a variety of other nerves by means of the plexus it forms around the internal carotid (i.e., promontorial) artery. One such branch is the deep petrosal (q.v.), which mainly arises from the lateral branch. In most cases, the majority of the fibers of the medial branch follow the promontorial artery through the anterior carotid foramen, where they form the cavernous plexus in the vicinity of the cavernous sinus and hypophysis.

Within the tympanic cavity the internal carotid nerve usually communicates, by means of fine filaments, with the tympanic branch of the glossopharyngeal (q.v.). (See DAVIES 1967:1249-1259.)

INTERNAL EAR

The internal ear consists of two parts: (a) the bony labyrinth, a series of cavities within the petrosal (vestibule, semicircular canals, and cochlea), and (b) the membranous labyrinth, a series of communicating membranous sacs and ducts (utricle and saccule, semicircular ducts, and duct of the cochlea), contained within the bony cavities. (DAVIES and DAVIES 1962:1302.)

JUGULAR FORAMEN
(FORAMEN JUGULARE)

The foramen of the osteocranium which provides passage for the internal jugular vein. It is not always found, for the fissura metotica (q.v.) is not always subdivided during the development of the skull.

LAMINA ALARIS

"Laterally each occipital arch is produced to form the lamina alaris, which extends behind and under the auditory capsule and ends ventrally in a well-developed paracondylar process for the rectus capitis lateralis" (DE BEER 1937:309).

LESSER PETROSAL NERVE
(N. PETROSUS MINOR, LESSER SUPERFICIAL PETROSAL N.)

The nerve formed by the union of filaments from the tympanic nerve (through the tympanic plexus) and a small branch (ramus anastomicus cum plexo tympanico) from the geniculate ganglion, which runs to the otic ganglion (see fig. I-4). The lesser petrosal nerve may be looked upon as the continuation of the tympanic nerve of the glossopharyngeal (q.v.). Contains secretomotor fibers for the parotid gland. (See DAVIES 1967:1328.)

LINEA SEMICIRCULARIS

The curved ridge of bone on the internal aspect of the lateral bullar wall in lemurs and tree shrews, the arc of which closely conforms to that of the ectotympanic.

MALLEOLAR SULCUS
(SULCUS MALLEOLARIS)

Shallow trough on the apex of the anterior crus of the ectotympanic which communicates with the Glaserian fissure, and along which the chorda tympani, gonial and Meckel's cartilage travel. (See VAN DER KLAAUW 1931:164.)

MANDIBULAR FOSSA
(FOSSA MANDIBULARIS: GLENOID FOSSA)

The concavity on the squamosal which lodges the head of the mandible. (DAVIES 1967:323.)

MASTOID CANALICULUS
(CANALICULUS MASTOIDEUS, OSTIUM INTROITUM)

The small foramen in the petrosal by means of which the auricular branch of the vagus enters the substance of the petrosal bone in some mammals. (See ANSON and DONALDSON 1973:7.)

MASTOID CAVITY

As used here, any distinct cavity which develops as a posterior inflation of the epitympanic recess and invades the bone forming the lateral wall of pars canalicularis (in some forms, the squamosal is invaded as well). In most cases, the cavity itself appears to correspond to the antrum, although the accessory spaces and cellules which may in turn develop from the antrum in other mammals do not always have counterparts in *Homo*, and vice versa.

MASTOID REGION

"...the posterior portion of the petrosal bone, essentially that portion of the bone posterior to a line joining the foramen stylomastoideum primitivum and foramen lacerum posterius" (MCDOWELL 1958:126).

The term "mastoid process" is avoided here since it is used in a great variety of senses. Where it is necessary to refer to an enlargment on the lateral part of the mastoid region, the neutral term "mastoid eminence" will be used.

MECKEL's CARTILAGE
(DORSAL CARTILAGE OF THE FIRST BRANCHIAL ARCH)

The well-developed bar of cartilage which forms from the first visceral (mandibular) bar. Its ventral end is involved in the formation of the mandible, while its dorsal end is initially continuous with the primordia of the malleus and the incus. Its intermediate part disappears or becomes a ligament. (See BAXTER 1953:289.)

Although an eponymous name, it is the only one with any currency in comparative embryology and is listed (but presumably as an unofficial alternative) in the NE.

MEDIAL ACCESSORY CAVITY

As used here, the space developed within the substance of the petrosal plate in lorises as a consequence of pneumatic activity originating from the supracochlear and mastoid cavities (and ultimately the epitympanic recess).

Although other authors (e.g., SABAN 1963, 1964) have regarded the medial accessory cavity as a part of the hypotympanic sinus, this usage is avoided because it suggests that the space inflates from the tympanic cavity proper.

MEMBRANOUS MEATUS

See EXTERNAL ACOUSTIC MEATUS.

MEMBRANOUS VENTRAL WALL OF THE TYMPANIC CAVITY

The early condition of the ventral wall, transitory in most mammals, when it consists only of the fibrous membrane of the tympanic cavity (q.v.) and the ventral part of the ectotympanic.

MIDDLE EAR
(AURIS MEDIA)

"The middle ear includes the tympanic cavity (cavum tympani), the tympanic antrum (antrum mastoideum), and the auditory tube (tuba auditiva). These constitute a continuous, irregular, pneumatic chamber and passage, located through the greater part of its extent in the temporal bone. The centrally located tympanic cavity is shut off from the external ear by the tympanic membrane (membrana tympani), and from the chamber that forms the internal ear by the structures that occupy the cochlear and vestibular windows" (ANSON and DONALDSON 1973:164).

MIDDLE MENINGEAL ARTERY
(A. MENINGEA MEDIA)

A branch, or merely the continuation of, the ramus superior of the stapedial artery which lies within the dura mater of the cranial cavity. (MCDOWELL 1958:126.)

NERVES OF THE PTERYGOID CANAL
(NN. CANALIS PTERYGOIDEI, VIDIAN NERVES)

The greater and deep petrosal nerves, during their passage through the pterygoid canal (fig. I-4).

It is universally held in textbooks of anatomy that these two nerves actually unite to form the vidian nerve (nerve of the pterygoid canal). HIGBEE (1975:9), however, points out that union is quite improbable. The deep petrosal is a bundle of postganglionic fibers of the sympathetic system which extends from the cranial cervical ganglion to the nasal mucosa and lacrimal gland without interruption. The greater petrosal nerve is composed of preganglionic fibers of the parasympathetic system extending from the superior salivary nucleus to the pterygopalatine ganglion. An anastomosis of the fibers, which are functionally anatagonistic, is inconceivable.

It can be demonstrated that the greater and deep petrosal nerves are separated by a sheath of connective tissue during their passage through the pterygoid canal in Homo. However, this sheath was not identifiable in the material available for this study. Nonetheless, I think it is necessary to accept HIGBEE's claim that the fibers of the two nerves maintain their independence. For this reason, I have emended the 'nerve' of the NA to 'nerves'.

OTIC GANGLION
(G. OTICUM)

A cephalic parasympathetic ganglion, topographically associated with the mandibular division of the trigeminal and lying immediately beneath the foramen ovale. It receives roots from the glossopharyngeal and facial nerves via the lesser petrosal nerve. (DAVIES 1967:1169.)

PARS CANALICULARIS

See AUDITORY CAPSULE.

PARS COCHLEARIS

See AUDITORY CAPSULE.

PERILYMPHATIC DUCT
(DUCTUS PERILYMPHATICUS, PERIOTIC DUCT, AQUEDUCTUS COCHLEAE)

"...is not a true duct but a potential space containing an arachnoid type of connective tissue and fluid. It begins in the scala tympani, near the cochlear window, and terminates in a funnel-shaped aperture situated medial to the jugular fossa" (ANSON and DONALDSON 1973:187).

See COCHLEAR CANALICULUS.

PETROSAL
(OS PETROSUM, PERIOTIC, PETROMASTOID)

"The entire bone formed by ossification of the otic capsule and its various processes. Because in man the petrosal, squamosal, and tympanic bones are fused into one, it is usual in human anatomy to refer to this bone as the 'petrous portion of the temporal bone'" (MCDOWELL 1958:126).

PETRO-OCCIPITAL SINUS

The name given by SABAN (1963:96) to the vein draining from the cavernous sinus, through the anterior carotid foramen, to the internal jugular vein.

Among the mammals studied here, the complete vessel is found only in lorises and cheirogaleid lemurs. In other cases, it is either absent or represented only by small emissary veins draining to the pharyngeal venous plexus (rather than to the internal jugular).

PETROSAL PLATE
(BULLA TYMPANICA PETROSI, PETROSAL BULLA)

The lamella formed by the union of the rostral and caudal tympanic processes of the petrosal (qq.v.), which forms part or all of the bony ventral wall in certain mammals.

PETROSQUAMOUS SINUS

The dural sinus which passes through the postglenoid foramen in order to drain into the external jugular vein. Absent or vestigial in man, but very common in mammals generally. (See BATSON 1975:15.)

PIRIFORM FENESTRA
(PYRIFORM FENESTRA)

This term (here emended to conform to the spelling rules of the NA) was originally coined by MCDOWELL (1958:128) to apply to the large vacuity in the roof of the middle ear of certain lipotyphlans. Here, the term will be broadened in meaning to include the large gap, seen in all fetal and a few adult mammals, which lies between the anterior end of the auditory capsule and its outgrowths (epitympanic wing of the petrosal, tegmen tympani) on the one hand and the epitympanic outgrowths of the sphenoid and squamosal on the other (see fig. I-3).

It is important to understand the relations of the piriform fenestra to the foramen caroticum primitivum and the later anterior carotid foramen. In the fetal mammal, the piriform fenestra is not continuous with the foramen caroticum primitivum, for the two are separated by the alicochlear commissure (q.v.; lorises and a few other mammals are special exceptions, but they do not change the generality of this observation). Hence it follows that the piriform fenestra in the fetus never gives passage to the promontorial artery.

With the ossification of the cranium, the piriform fenestra experiences different fates in different species. In the adults of many mammals, the fenestra is largely closed over as a result of the growth of the epitympanic wings; in these instances, its original position will be indicated by sutures alone (petrosphenoid, medial petrosquamosal). In the adults of some mammals (e.g., many soricomorphs), however, the growth of the epitympanic wings is not so extensive and a membrane-covered deficiency of varying size and relations will remain. In such cases, the remaining part of the piriform fenestra and the anterior carotid foramen will appear to be continuous in macerated skulls. The large gap thus produced is often called the "middle lacerate foramen", but the lateral part of this foramen is obviously not involved in the passage of the promontorial artery and has nothing to do with the original foramen caroticum primitivum. For this reason, the term "middle lacerate foramen" is not employed here.

POSTERIOR BASICAPSULAR COMMISSURE
(BASIVESTIBULAR COMMISSURE)

The transitory, cartilaginous bridge which joins the posteromedial side of pars cochlearis to the basal plate of the central stem. It separates the basicapsular fenestra from the fissura metotica. Occasionally absent. (See STARCH 1967:444.)

POSTERIOR CAROTID FORAMEN

The foramen of ingress by means of which the internal carotid artery enters the posterior part of the middle ear.

"The posterior carotid foramen lies generally in the hinder part of the bulla, a little more on the medial side than the stylomastoid foramen. It is not always present, first, since there is not always a bulla, as in monotremes, in *Sorex*, *Orycteropus*, and others; secondly, since the ventral wall of the bulla is sometimes partly membranous" (VAN DER KLAAUS 1931:179).

In addition to the internal carotid artery, the foramen also transmits the internal carotid nerve, and, occasionally, other small vessels.

POSTERIOR CONTINUATION OF THE CRISTA PAROTICA.

See CRISTA PAROTICA.

POSTERIOR LACERATE FORAMEN
(FORAMEN LACERUM POSTERIUS)

The foramen in the rear part of the osteocranium which provides passage for the IX, X, and XI cranial nerves (and the internal jugular vein as well in forms which lack a separate jugular foramen). It is the successor of the fissura metotica of the chondrocranium (q.v.).

Although the term "middle lacerate foramen" is not used here (see PIRIFORM FENESTRA), the comparative "posterior" is retained in order to avoid confusion.

POSTGLENOID FORAMEN

The foramen situated behind the mandibular fossa which transmits the persistent petrosquamous sinus (q.v.).

POSTGLENOID PROCESS

Following MCDOWELL (1958:127), any kind of projection of the squamosal which receives the condyle of the mandible. However, in some forms the "true" postglenoid process (see PROCESSUS POSTGLENOIDEUS) has probably been functionally replaced by the entoglenoid process (q.v.).

POSTTYMPANIC PROCESS

A process formed by the squamosal which is related to the posterior margin of the external acoustic meatus. (See VAN KAMPEN 1905:343.)

PROCESSUS ALARIS
(PROCESSUS BASITRABECULARIS)

A laterally-projecting outgrowth which chondrifies from the hypophyseal plate of the central stem, and which communicates laterally with the alicochlear commissure and with the basal end of the ala temporalis. (See ROUX 1947:178.)

PROCESSUS POSTGLENOIDEUS

"Here used to mean a 'true postglenoid process' homologous with that of man. That is, a process of the squamosal on the zygomatic arch, near the juncture of the latter with the braincase, abutting against the posterior surface of the dentary condyle and attacking the latter from directly posterior. The process lies mainly or entirely dorsolateral to the Meckelian cartilage and chorda tympani and is anterior or anterolateral to the postglenoid foramen (when the latter is present)" (MCDOWELL 1958:127).

PROCESSUS RECESSUS

The cartilaginous process or bar which extends from the posteroventral surface of the pars cochlearis to the anteroventral surface of pars canalicularis and which provides the floor of the recessus scalae tympani. It helps to define medial and lateral apertures for the recessus, which become the cochlear canaliculus and fenestra cochleae in later ontogeny. (See DE BEER 1929; and FRICK 1952, 1954.)

The processus recessus becomes increasingly complex structurally as it develops and ossifies. From the vantage point of adult middle ear anatomy, its relations are most easily understood if it is remembered that it forms the medial wall of the apertura fossulae fenestrae cochleae (q.v.).

PROCESSUS STYLIFORMIS

"The processus styliformis is a process of the fore end of the auditory bulla and forms the prolongation of the bony Eustachian tube" (VAN DER KLAAUW 1931:133). The equivalent of the processus muscularis of veterinary anatomy (SISSON 1938:63), it gives purchase to the tensor and levator palati muscles.

PROMONTORIAL ARTERY
(A. PROMONTORII, PROMONTORY A., LATERAL INTERNAL CAROTID A.)

The medial of the two branches formed by the bifurcation of the internal carotid artery after it enters the middle ear, the other branch being the stapedial artery. From its origin, the promontorial artery traverses the ventral surface of the promontory, passes over the latter's anterior pole, and enters the cranial cavity in order to join the circulus arteriosus.

This artery may be considered to be the distal segment of, and is therefore often called, the internal carotid.

PROMONTORY
(PROMONTORIUM)

The rounded prominence within the middle ear formed by the projection outward of the first turn of the cochlea. (DAVIES 1967:1321.)

It corresponds to the major portion of the pars cochlearis, except, of course, for the latter's dorsal (cerebral) surface (which is not visible from the middle ear).

In the text, anterior and posterior poles of the promontory are distinguished. The former contains the swollen apex of the cupula cochleae, while the latter includes the region housing the fossula fenestrae cochleae.

PTERYGOID BONE
(OS PTERYGOIDEUM)

An independent, intramembranous ossification which fuses with the alisphenoid and basisphenoid. Its descending portion forms the medial pterygoid lamina, while its posterior end sometimes takes part in the construction of the tympanic process of the basisphenoid and adjacent incisure or groove for the auditory tube. (See DE BEER 1937:366.)

PTERYGOID CANAL
(CANALIS PTERYGOIDEUS, VIDIAN CANAL)

A canal of the osteocranium, usually passing along or through the site of fusion of the pterygoid and basisphenoid, which transmits the nerves of the pterygoid canal and occasionally an accompanying artery (artery of the pterygoid canal, q.v.). (See DE BEER 1937:314.)

The mere presence of a pterygoid canal in a dried skull or a fossil does not conclusively establish that the artery of the pterygoid canal was present, in the absence of other evidence. There is no way of determining in such cases whether the canal contained only nerves or the artery as well.

PTERYGOPALATINE GANGLION
(G. PTERYGOPALATINUM, SPHENOPALATINE G.)

The largest of the cephalic parasympathetic ganglia topographically associated with the trigeminal nerve. It is situated within the pterygopalatine fossa, close to the sphenopalatine foramen and in front of the anterior orifice of the pterygoid canal. (DAVIES 1967:1149-1150.)

See NERVES OF THE PTERYGOID CANAL.

RAMUS INFERIOR (OF THE STAPEDIAL ARTERY)

A branch of the (proximal) stapedial artery which runs across the anterior part of the roof of the tympanic cavity to enter the temporal fossa, close to the position of the foramen ovale. (GREGORY 1920:172.)

Once within the temporal fossa, this artery (which often obliterates during ontogeny) may anastomize with various vessels (see BUGGE 1974). However, its major areas of supply generally include the upper and lower jaws (through the ramus infraorbitalis and ramus mandibularis).

See fig. I-4.

RAMUS POSTERIOR (OF THE STAPEDIAL ARTERY)

A branch of the (proximal) stapedial artery which is released by the parent vessel just before the latter enters the obturator foramen of the stapes. It passes backwards out of the tympanic cavity in close relation to the facial nerve and the stapedius muscle. (See VAN VALEN 1966:9-10.)

This vessel is not usually identified for recent mammals. However, among the forms studied here, it is present in (?all) tenrecs, Solenodon, and at least young stages of Erinaceus. It may terminate in the stapedius muscle, or have a more extensive distribution which includes the lambdoidal region of the skull and the auricle.

See fig. I-4.

RAMUS SUPERIOR (OF THE STAPEDIAL ARTERY)

A branch given off by the (proximal) stapedial artery after the latter passes through the obturator foramen of the stapes, usually at the same time as the ramus inferior is released. The ramus superior passes through the roof of the tympanic cavity in order to enter the cranial cavity.

Within the cranial cavity, this artery (which rarely obliterates during ontogeny) may, like the ramus inferior, form various anastomoses with other vessels (see BUGGE 1974). Typically, however, it feeds the dura (by means of the middle meningeal) and the orbital area (by means of the frontal, ethmoidal, lacrimal and ciliary arteries).

See fig. I-4.

RECESSUS MEATUS

As conventionally used, the more or less well-defined, circular fossa produced external to the ventral part of the tympanic membrane as a result of the lateral broadening of the ectotympanic (or the entotympanic or petrosal plate). (See VAN KAMPEN 1905:358; VAN DER KLAAUW 1931:137.)

In fact, the recessus is never an empty space, but is always filled with the tissues of the membranous meatus.

RECESSUS SCALAE TYMPANI

The area in which the cul-de-sac of the scala tympani (a fluid-filled space of the perilymphatic labyrinth) is situated. In the adult mammal, the recessus lies behind the lower part of the secondary tympanic membrane. (See RICHANY, ANSON and BAST 1975:94-96.)

See PROCESSUS RECESSUS.

REICHERT's CARTILAGE
(DORSAL CARTILAGE OF THE SECOND BRANCHIAL ARCH)

The well-developed cartilage which forms from the second visceral (hyoid) bar. It is initially in continuity with the primordia of the crura of the stapes and the long crus of the incus. These associations are later lost, and the dorsal end of the cartilage then fuses with the crista parotica (q.v.) of the developing otic capsule. Ventrally, the cartilage articulates with the thyrohyal (third visceral bar).

There is great variety in the development of Reichert's cartilage in mammals. It may ossify from as many as four separate centers (in proximal to distal order, tympanohyal, stylohyal, ceratohyal, and hypohyal), or one or more of these centers may fail to appear. Also, two or more ossifications may fuse (as in man, where the styloid process represents the fused tympanohyal and stylohyal). (See CORSY 1933:234-260.)

For the association of Reichert's cartilage with the crista parotica, see TYMPANOHYAL.

Regarding the use of an eponymous name in this instance, see MECKEL's CARTILAGE.

ROSTRAL ENTOTYMPANIC

An entotympanic which arises in the rostral part of the ventral wall of the tympanic cavity. It may be intimately fused with the cartilage of the tube during the early phases of its development. See ENTOTYMPANIC(S).

ROSTRAL TYMPANIC PROCESS OF THE PETROSAL
(PROCESSUS TYMPANICUS PETROSI CAUDALIS)

As used here, any bullar wing which arises primarily from the ventral surface of the promontory of pars cochlearis.

It makes its first appearance as a periosteal outgrowth of the promontory after the latter is already highly ossified. Typically, it lacks preformation in primary cartilage, although secondary cartilage may appear within it later in ontogeny.

In the forms considered here, it apparently never has its own center of ossification.

See PETROSAL PLATE.

SECONDARY TYMPANIC MEMBRANE
(MEMBRANA TYMPANI SECUNDARIA)

The trilaminar membrane which closes the fenestra cochleae and separates the scala tympani from the tympanic cavity. (RICHANY, ANSON and BAST 1975:96.)

SEPTUM

As used here, any cartilaginous or bony revetement projecting into the middle ear spaces. Septa may be complete or incomplete, depending on whether they define whole compartments or merely provide relief within large cavities. They are often associated with canals for blood vessels.

STAPEDIAL ARTERY
(A. STAPEDIA)

"The stapedial artery develops early from an anastomosis through the stapes blastema, between the rudiments of the first and second aortic arches, and fully elaborated comprises a supraorbital branch supplying the dura and orbit and an infraorbital branch and mandibular branch supplying the upper and lower jaws respectively" (BUGGE 1974:15).

If preserved, it appears as the lateral of the two branches formed by the bifurcation of the internal carotid in the adult. From its origin it passes through the obturator foramen of the stapes and ascends to the roof of the tympanic cavity. It may release up to three branches during its course through the middle ear. Here, the traditional names for these branches are used: ramus inferior ("distal part of the stapedial stem" of BUGGE 1974), ramus superior (intratympanic portion of ramus supraorbitalis of BUGGE 1974), and ramus posterior (not named or described by BUGGE 1974).

In order to avoid ambiguity, the section of the stapedial artery extending from its origin to the point of bifurcation into inferior and superior rami (or to the place where it leaves the tympanic cavity if no bifurcation occurs) will be termed the "proximal part of the stapedial stem" or simply, "proximal stapedial".

STAPEDIUS MUSCLE
(M. STAPEDIUS)

The small muscle which originates from the rear of the otic capsule, medial to the prominence of the lateral semicircular canal, and which inserts into the neck of the stapes by means of the stapedius tendon. It is innervated by the stapedius nerve of the facial. Its action is to draw the head of the stapes backward and rotate the anterior end of the base or footplate outward, thus tensing the anular legament. (See SISSON 1939:900.)

STYLOMASTOID FORAMEN
(FORAMEN STYLOMASTOIDEUM)

The foramen by means of which the facial nerve finally leaves the middle ear. Two conditions of this foramen are usually distinguished. The "foramen stylomastoideum primitivum" (BROMAN 1899) is not a foramen at all, in the sense of an aperture enclosed by bone or cartilage. Instead, it marks the place where the facial nerve penetrates the fibrous tissue adjacent to Reichert's cartilage (or the tympanohyal) in order to descend into the upper neck. The foramen stylomastoideum primitivum is a constant feature of the mammalian fetus, and is also found in the adult stage of forms in which tympanic processes fail to enclose the facial nerve at its point of departure from the middle ear.

The "foramen stylomastoideum definitivum" may be thought of as the ontogenetic successor of the foramen stylomastoideum primitivum. It is properly identified only in those cases where the petrosal (or, occasionally, the entotympanic or ectotympanic) alone or in combination with the tympanohyal forms a definite aperture.

Where useful, the primitive and definitive conditions of the foramen are distinguished in the text. Where not, the neutral term "stylomastoid foramen" will be used (cf. MCDOWELL 1958:128).

SUPRACOCHLEAR CAVITY

A term coined here to refer to the space which develops from the medial part of the epitympanic recess through the pneumatization of the bone of the dorsal (cerebral) wall of pars cochlearis.

See MEDIAL ACCESSORY CAVITY.

TEGMEN TYMPANI

An initially-cartilaginous process of the anterolateral edge of the canalicular part of the auditory capsule which provides part of the roof of the tympanic cavity in mammals. The root of the tegmen is crossed by the facial sulcus. (See DE BEER 1929:418.)

TENSOR TYMPANI MUSCLE
(M. TENSOR TYMPANI)

The small muscle which originates from the sphenoid, extensions of the cartilage of the tube, petrosal, and, occasionally, from the membrane covering the piriform fenestra. It lies along the dorsomedial wall of the tympanic cavity covered by a dense layer of mucous membrane and extends posteriorly in the fossa of the tensor tympani to approximately the level of the apertura fenestrae vestibuli; along this course or in front of the apertura it bends laterally and attaches to the muscular process on the inner surface of the neck of the malleus. (HENSON 1961:163.)

It is innervated by a branch of the mandibular division of the trigeminal nerve (n. tensoris tympani) through the otic ganglion. Its action is to draw the handle of the malleus inward, thus tensing the tympanic membrane.

TRIGEMINAL GANGLION
(G. TRIGEMINALE, GASSERIAN G., SEMILUNAR G.)

The large ganglion which gives rise to the ophthalmic, maxillary and sensory part of the mandibular nerve. It is accommodated in the prominent fossa (impressio trigeminalis) on the dorsal (cerebral) aspect of the alisphenoid and contiguous part of the petrosal. (See JOHNSTON et al. 1958:1100.)

TRIGEMINAL (V) NERVE
(N. TRIGEMINUS)

The largest cranial nerve. It is the sensory nerve of the face, the greater part of the scalp, the teeth, the mouth and the nasal cavity, and the motor nerve of the muscles of mastication and soem other muscles. It divides into three branches, the ophthalmic (V_1), the maxillary (V_2) and the mandibular (V_3). (DAVIES 1967:1143.)

TUBAL CANAL (FORAMEN, GROOVE)

The aperture or incisure through which the auditory tube enters the tympanic cavity.

TUNICA MUCOSA OF THE TYMPANIC CAVITY
(MUCOUS MEMBRANE OF THE TYMPANIC CAVITY)

The membrane which lines the walls and spaces of the middle ear and invests its exposed contents (e.g., ossicles, muscles, nerves, arteries). The lining is continuous anteriorly with the mucosa of the auditory tube and posteriorly with that of the mastoid cavity (if formed). (See ANSON and DONALDSON 1973:169.)

TYMPANIC CANALICULUS
(CANALICULUS TYMPANICUS)

The small foramen in the petrosal by means of which the tympanic nerve of the glossopharyngeal enters the tympanic cavity. (ANSON and DONALDSON 1973:10.)

TYMPANIC CAVITY

In the adult, the osseous chamber of the basicranium which contains the cavum tympani (q.v.).

Included within it are the structures of the middle ear concerned with the actual mechanics of transforming air vibrations into vibrations strong enough to move the fluids of the inner ear: the auditory ossicles, ossicular muscles, and the fenestrae vestibuli and cochleae. (WEBSTER 1966:452.)

TYMPANIC MEMBRANE
(MEMBRANA TYMPANI, EARDRUM)

The membranous partition between the external and middle ears which is involved in the conduction of sound to the ossicular chain.

It consists of two portions, the pars tensa (attached to the tympanic sulcus of the ectotympanic) and the pars flaccida (lying between the tympanic notch and the adjacent part of the roof of the external acoustic meatus).

These two portions differ in their composition. Pars flaccida is bilaminar (formed by the skin of the meatus and the tunica mucosa), while pars tensa is trilaminar (formed by the two preceding tissues and an intervening, double-layered stratum). (See ANSON and DONALDSON 1973:164-165.)

TYMPANIC MUCOID TISSUE

The tissue which initially fills much of the presumptive tympanic cavity. It is at first embryonic mesoderm, then differentiates into a myxomatous (mucoid) tissue which undergoes resorption as the early cavum tympani expands and pushes it aside. It is mostly resorbed by late fetal life (in Homo), although some remains as the so-called mucoperiosteal layer of the tunica mucosa. (PEARSON and JACOBSON 1967:6-9.)

TYMPANIC NERVE
(N. TYMPANICUS, N. OF JACOBSON)

The tympanic nerve arises from the distal (or inferior) ganglion of the glossopharyngeal and passes upward between the petrosal and the ectotympanic to reach the tympanic cavity. Within the tympanic cavity

it sends branches to the tympanic plexus. (SISSON 1938:825.)
See fig. I-4 and LESSER PETROSAL NERVE.

TYMPANIC NOTCH
(INCISURA TYMPANICA, NOTCH OF RIVINUS)

See ECTOTYMPANIC.

TYMPANIC PROCESS

A general term used here for any bony or cartilaginous outgrowth which contributes to the floor of the middle ear.
See EPITYMPANIC WING and fig. I-2.

TYMPANIC PROCESS OF THE ALISPHENOID

An outgrowth of the rear of the alisphenoid which bounds the anterior end of the tympanic cavity in certain mammals (e.g., many marsupials, lipotyphlans). See fig. I-2.

TYMPANIC PROCESS OF THE BASISPHENOID

An outgrowth of the lateral margin of the basisphenoid which helps to bound the medial side of the tympanic cavity. It may be insignificant in size (e.g., elephant shrews), or may form most of the bony ventral wall (e.g., golden moles). The ontogenetic evidence indicates that its anterior part almost always includes material derived from the pterygoid bone. See fig. I-2.

TYMPANIC SULCUS
(SULCUS TYMPANICUS)

The groove channeling the inner circumference of the ectotympanic, to which the tympanic membrane is attached by means of the fibrocartilaginous ring (anulus fibrocartilagineus). (ANSON and DONALDSON 1973: 165.)

TYMPANOHYAL

The most proximal of the ossification centers which may form in Reichert's cartilage. It is known by a variety of names, including laterohyal, epihyal, and 'hyoid' process. Usually indistinguishably fused with the petrosal (crista parotica) by the late fetal stage. (See DE BEER 1937:372.)

It should be noted that it is conventional to call any projection immediately in front of the stylomastoid foramen a 'tympanohyal' (in the adult), but this implies a knowledge of the method of ossification of Reichert's cartilage which is often lacking. The dorsal part of the cartilage may fail to ossify independently, and an observed projection may actually consist of petrosal material.

VAGUS (X) NERVE
(N. VAGUS)

The cranial nerve with the most extensive course and distribution, since it passes through the neck and thorax to the abdomen. Issues from the posterior lacerate foramen (q.v.). (JOHNSTON et al. 1958: 1130.) (See fig. I-4.)

VERTEBRAL ARTERIES
(AA. VERTEBRALES)

See BASILAR ARTERY.

VISCERAL BAR

Term for the entire block of condensed mesenchymal tissue (or later, cartilaginous tissue) which forms in a given branchial arch. (PEARSON and JACOBSON 1967:16-17.)

Thus, Reichert's cartilage and its subdivisions, the manubrium of the malleus and the long crus of the incus are all products of the second visceral bar.